

# BOTANICAL GAZETTE

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## THE EFFECT OF THE PRESENCE OF INSOLUBLE SUBSTANCES ON THE TOXIC ACTION OF POISONS.<sup>1</sup>

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It has been repeatedly observed in connection with the poisonous action of dissolved substances that the harmful effects are much more marked when the roots of the plants under test are immersed in the solutions than when these are grown in sand cultures which are watered with like or even more concentrated solutions (1). Upon this point the practice advocated by NÄGELI (2) for removing traces of metals from distilled water may be cited. When to distilled water, rendered harmful for algae by the presence of traces of copper, crushed graphite, shredded filter paper, paraffin shavings, and other insoluble substances are added, the copper is removed from the water by some process dependent to a degree upon the amount of surface offered by the insoluble substance.

In connection with experiments carried out in 1902 by TRUE and GIES (3) at the Plant Physiological Laboratory at Woods Hole, Mass., on the modification of the action of poisons by the presence of other compounds, some preliminary experiments were made bearing on the effect exerted by the presence of insoluble materials on the behavior of seedlings of *Lupinus albus*. A concentration of copper sulfate was experimentally determined in which growth for twenty-four hours was possible, though at a somewhat diminished rate. When to duplicate cultures insoluble substances were added, in nearly all cases a marked increase in the growth rate was noted.

<sup>1</sup> After this paper was prepared, the line of argument and the evidence were submitted to Dr. LYMAN J. BRIGGS, physicist of the Bureau of Soils, U. S. Department of Agriculture. He has most generously given us the benefit of his special advantages.



The same volume of solution was used in each case and the same amount of copper was present in each culture. In some cases a copper-containing solution, in itself harmful, gave a marked stimulation when the insoluble material was added. In other cases the increase in the growth rate was less marked or, in two cases, absent. The general trend of the evidence, however, was clearly in favor of NÄGELI's conclusion that insoluble bodies in some way remove from action limited quantities of the copper in the solutions.

During the summer session of 1903, C. S. OGLEVEE, of the John Milliken University of Lincoln, Illinois, while working in the Plant Physiological Laboratory at Woods Hole, repeated the experiments above described and extended their scope. He used the radicles of seedlings of *Lupinus albus* as test objects.

The insoluble substances used represented several types of substances, having little in common beyond their insolubility. In making a choice of these the suggestions of NÄGELI were again acted upon. In experimenting with these different insoluble or difficultly soluble materials we attempted to use such quantities of each substance as would offer, as nearly as possible, like surfaces to the solutions. It is improbable, however, that even approximate accuracy was reached on account of the different sizes and shapes of the particles. Clean sea sand of rather coarse texture was used most frequently. It was selected from the cleanest parts of the beach near Woods Hole, boiled for about an hour in dilute hydrochloric acid, then thoroughly washed in fresh water and finally in distilled water.

Powdered Bohemian glass was prepared by crushing up some flasks and beakers that had been cracked or broken. This crushed glass was repeatedly washed in distilled water for a long time before being made use of in the experiment. It is a matter of common information that glass of this type is not strictly insoluble in water, and traces of the more soluble constituents were doubtless present in experiments with this substance.

Filter paper was also used. Cut filters of good commercial grade were shredded into distilled water and digested for a protracted period with several changes of water before use.

Powdered anthracite coal was also tried after a thorough treat-

ment with distilled water. It was noted that gas bubbles were repeatedly found over the surface of the submerged particles of coal and that after being removed by thorough stirring these would again form. This evolution of gas continued during the entire time in which the coal was under observation. The nature of the gas was not determined.

Finely divided pure paraffin of high melting point was also made use of. Investigations made on the effect of paraffin on the electrical conductivity of pure water have shown that paraffin does not noticeably increase the conductivity and seems to be practically insoluble in water.<sup>2</sup>

Owing to the lightness of the paraffin, the finely divided particles floated on the surface of the solutions, but owing to the small spaces between the pieces, the solution rose by capillary action among them and they became, in effect, submerged in the solutions.

At the suggestion of Dr. HENRY KRAEMER, of the Philadelphia College of Pharmacy, unruptured potato starch grains were tried. A stock was freshly prepared from potatoes by crushing and washing out the starch grains, care being taken to avoid other structures from the tuber. The starch thus obtained was dazzlingly white and distilled water in which a portion of the material was allowed to stand for some time gave no starch reaction when treated with iodine. By rubbing up a little of the same starch with a little distilled water a strong starch reaction appeared on adding iodine solution. Careful washing removed all traces of other substances.

The toxic substances receiving most attention in this investigation were those which have been shown to possess great poisonous activity. Copper sulfate, silver nitrate, mercuric chlorid, hydrochloric acid, sodium hydroxid, thymol, and resorcinol may be especially mentioned. The chemicals in the case of the heavy metals were Merck's guaranteed reagent grade. The remaining compounds were recognized makes of chemically pure quality. The solutions were made up with such care as the apparatus of the

<sup>2</sup> We are informed that investigations by F. K. CAMERON and LYMAN J. BRIGGS of the Bureau of Soils, U. S. Department of Agriculture, show that high grade paraffin of high melting point, of the sort here used, has but a minimal effect on the electrical conductivity of distilled water in which it is placed.

laboratory permitted, and we believe that the concentrations were usually accurate.

The method of operation consisted essentially in suspending the seedlings on glass rods in the solutions concerned for twenty-four hours each in each experiment, in such a manner as to immerse the radicles. In nearly all cases the plants were under observation at least forty-eight hours. Never less than four seedlings were used in any experiment and frequently more were employed. The average is taken as the result. The seedlings were placed with the roots in the solutions, care being taken to use plants in like stages of development. Growth was measured from an India ink line placed 15 mm from the tips of the roots at the beginning of the experiment. During the exposure to the action of the solutions the culture dishes stood in diffused light. The influence of variable factors, such as temperature, was kept track of by check cultures in distilled water.

The water was distilled in an apparatus lined with block tin and was not, therefore, of the highest purity. It was consistently used, however, throughout the season and forms a constant factor in all experiments. Beakers of 300<sup>cc</sup> capacity and of similar shape were used.

In studying the effect of the presence of insoluble substances on the poisonous activity of the compounds mentioned, a quantity of the sand, filter paper, or paraffin was generally used equal to about one-third of the volume of the solution of the poisonous agent. Thus, in the beakers used for these cultures about two-thirds of the depth of the solution was to be seen *above* the level of the sediment in all but the floating paraffin, in which case the order was inverted.

After marking the roots and introducing them into the solutions under study, the plants were set away for twenty-four hours, at the end of which time they were again measured and the amount of growth noted. Usually, to avoid further complications arising in the case of prolonged experiments, the results due to exposure of twenty-four hours were sought.

#### EXPERIMENTAL RESULTS.

The first step taken with each toxic agent was to determine approximately the maximum concentration permitting the survival of the plants. This was then followed by a study of the results following the introduction of the particular insoluble substance under study.

The first group of toxic agents tested were exclusively electrolytes, which at the very advanced degree of dilution here seen may be regarded as acting chiefly as ions. The possible presence of a residuum of molecules, especially in the case of  $\text{HgCl}_2$ , is of no particular significance for the present discussion. Concentrations are always cited in terms of parts of a gram-molecule of the substance in question per liter of solution.

*Mercuric chlorid.*

Preliminary experiments were made to determine the toxic activity of the solution in the absence of insoluble substances. A concentration was then selected at which growth, although greatly depressed, is still possible before death results, and parallel cultures were then made in these concentrations both with and without the insoluble substance. The following table summarizes the results, growth made being indicated in millimeters:

TABLE I.  
MERCURIC CHLORID.

1 gram-molecule	Growth in 24 hrs.	Growth in 70 hrs.
18,000 liters.....	2.0mm	6.5mm
18,000 + 75 <sup>gm</sup> sand.....	6.0	21.0
20,000 liters.....	10.0	28.5
20,000 + crushed glass.....	16.9	40.0
Check in water.....	12.0	16.0

It is clear that the presence of both sand and crushed glass here modifies very markedly the toxic influence of the mercuric chlorid. This amelioration is evident not only during the first twenty-four hours of the experiment, during which the roots were exposed to the corrosive sublimate solution, but also during the following period of nearly two days, during which the roots were placed in tap water. The course of the check experiment shows that the presence of the insoluble bodies exerts a clearly stimulating effect on the roots. The same may be seen in a less marked degree in the more dilute solution lacking the insoluble substance.

*Silver nitrate.*

The above methods were applied to silver nitrate in a large number of dilutions, with somewhat less marked results.

TABLE II.  
SILVER NITRATE.

1 gram-molecule	Growth in 24 hrs.	Growth in 48 hrs.
JULY 22		
150,000 liters.....	7.0mm	8.0mm
150,000 liters + sand.....	17.0	34.0
200,000 liters.....	13.0	22.0
200,000 liters + sand.....	16.0	31.0
200,000 liters + starch.....	13.0	22.0
250,000 liters.....	10.0	16.0
250,000 liters + sand.....	15.0	(weak seedlings.) 32.0
Water, distilled.....	16.0	19.0
Water + sand.....	12.0	14.0
AUGUST 20		
250,000 liters.....	16.0	
250,000 liters + sand.....	16.0	
300,000 liters.....	16.0	
300,000 liters + sand.....	18.0	
Distilled water.....	14.0	
Distilled water + sand.....	12.0	
AUGUST 17		
350,000 liters.....	14.0	
350,000 liters + sand.....	12.0	
350,000 liters + glass.....	14.0	
350,000 liters + filter paper.....	19.0	
Distilled water.....	12.0	
Distilled water + filter paper.....	13.0	
AUGUST 14		
350,000 liters.....	10.0	18.0
350,000 liters + sand.....	17.0	34.0
Distilled water.....	9.0	15.0

A study of the numerical data shows that in four cases out of ten, in which the active solutions with and without the solids are compared, no increased growth rate appears in the presence of the solid. In three out of four cases marked by the absence of an acceleration, the resulting growth rate agrees with that of the roots in the solutions lacking solids. In one case out of ten there is a retardation seen to follow the introduction of the solid. If we examine the six cases in which an acceleration followed the introduction of the solid, the sum of the differences in favor of the cultures containing the solids is 32<sup>mm</sup>. Thus, seen collectively, the increase in growth rate due to the presence of the solids is very marked. Since no experiments were made for contrasting the efficiency of the various solids used, we cannot say in how far the differences in the nature or in the quantity of the

solids present may be responsible for the differences noted. In some degree, also, slight differences in handling during the experiment and also individual differences in the roots produce slight, uncontrolled effects.

*Copper sulfate.*

A greater number of experiments were made with copper sulfate than with any other substance. This has an added interest because of NÄGELI'S (2, p. 23) experiments with *Spirogyra* in extremely dilute solution. NÄGELI found that distilled water prepared by means of a copper still may contain enough metal to produce fatal results with *Spirogyra*. The remedy proposed as a laboratory expedient for making water thus prepared fit for use was to put finely divided insoluble bodies into the water. The results obtained with copper sulfate follow. Although there is considerable repetition and some experiments are not completely carried out, it seems desirable to present all the evidence, showing as it does the range of variation in the results:

TABLE III.  
COPPER SULFATE.

1 gram-molecule	Growth in 24 hrs.	Growth in 70 hrs.
JULY 8		
32,768 liters.....	2.0mm	Dead
32,768 liters + glass.....	2.0	"
49,152 liters.....	3.0	"
49,152 liters + sand.....	4.0	"
Distilled water.....	12.0	17.0mm
JULY 10		
50,000 liters.....	1.0	Dead
50,000 liters + sand.....	14.0	28.0mm
65,000 liters.....	12.0	28.0
65,000 liters + sand.....	16.0	32.0
JULY 13		
35,000 liters.....	1.0	Growth in 48 hrs. Dead
35,000 liters + sand.....	7.0	12.0mm
40,000 liters.....	2.0	Dead
40,000 liters + sand.....	5.0	9.0mm
50,000 liters.....	2.0	Dead
50,000 liters + sand.....	11.0	17.0mm
Distilled water.....	10.0	13.0
Distilled water + sand.....	8.0	15.0

TABLE III—*Continued*

1 gram-molecule	Growth in 24 hrs.	Growth in 70 hrs.
JULY 16		
35,000 liters.....	4.0	Dead
35,000 liters + glass.....	10.0	17.0 <sup>mm</sup>
35,000 liters + filter paper.....	18.0	32.0
Distilled water.....	12.0	15.0
Distilled water + glass.....	9.0	16.0
Distilled water + filter paper.....	12.0	21.0
Distilled water + glass wool.....	16.0	29.0
JULY 20		
35,000 liters + starch.....	12.0	
35,000 liters + glass wool.....	5.0	
Distilled water.....	14.0	
Distilled water + sand.....	12.0	
JULY 24		
35,000 liters.....	3.0	Growth in 72 hrs.
35,000 liters + paraffin.....	8.0	
Distilled water.....	12.0	
JULY 29		
35,000 liters.....	1.0	
35,000 liters + glass.....	4.0	
JULY 30		
35,000 liters.....	1.0	
35,000 liters + paraffin.....	3.0	
JULY 31		
35,000 liters.....	1.0	Dead
35,000 liters + garden soil.....	13.0	19.0 <sup>mm</sup>
Distilled water.....	14.0	19.0
Redistilled water.....	15.0	16.0
AUGUST 5		
35,000 liters.....	2.0	
35,000 liters + sand.....	7.0	
35,000 liters + paraffin.....	5.0	
Distilled water.....	12.0	
AUGUST 10		
35,000 liters.....	2.0	Growth in 48 hrs.
35,000 liters + 40 <sup>grms</sup> sand.....	7.0	Dead
35,000 liters + 80 <sup>grms</sup> sand.....	10.0	Living
35,000 liters + 120 <sup>grms</sup> sand.....	16.0	Good condition
35,000 liters + 160 <sup>grms</sup> sand.....	13.0	Excellent
35,000 liters + 200 <sup>grms</sup> sand.....	12.0	Thrifty
		Thrifty

Several facts seem to be clearly brought out in the above exhibit. Lupine roots are unable to survive an exposure of twenty-four hours to a concentration of copper sulfate in which a molecular weight is dissolved in much less than 60,000 liters—a point which has been

repeatedly observed before (3, 4). When, however, to a solution containing nearly or quite twice this amount of the copper salt, finely divided insoluble bodies, like quartz sand, crushed glass, and filter paper are added, the toxic action is so far diminished as to permit not only an increased growth before death takes place but even vigorous survival. In case the amount of copper is diminished, an advantage is regularly found in favor of the cultures containing the solid body.

In the case of the culture containing the garden earth, the effect of a common type of soil containing considerable soluble matter was desired. Of course chemical reactions have entered here, but at this great dilution the copper probably still existed in the ion condition. Here, too, the introduced soluble material may have had its own direct action on the organisms.

The action of paraffin is marked in every case but in a somewhat less degree than in the other cases noted. The paraffin offered some slight difficulty of method which may account somewhat for the fact observed. Although hard paraffin was used, it was found difficult to shave or chop it up into particles of the desired degree of minuteness. Thus less surface was exposed to the solution than in the other substances used. Its lightness, too, tended to buoy it up upon the surface of the solution, and prevent a thorough mingling. This was remedied in part by the tendency of the solution to rise by capillary action among the floating particles. It was also found practicable to hold the paraffin under, to a considerable degree, by means of pressure on the surface of the floating mass.

The effect of solids on growth in the distilled water was tried in control experiments, the general result seeming to indicate that the plants are not favored by this presence. Redistilling from glass, discarding the first half of the distillate and leaving a third of the original volume in the retort, seems to yield a product having no advantage over the water but once distilled.

In all of the toxic substances thus far considered, we have had to do exclusively with electrolytes, therefore, at the high dilutions concerned, with ions. Experiments were made with a few non-electrolytes in order to ascertain whether the ionization of the molecule may be a necessity for the observed decrease in the poisonous action of the presence of insoluble substances.



*Non-electrolytes.*

Those tested in this connection were phenol, resorcinol, and thymol. The investigations by BADER (5) on the conductivity of phenyllic compounds showed that in the substances here concerned no ionization is to be found. We have, therefore, here to do with entire molecules.

TABLE IV.  
PHENOL.

1 gram-molecule	Growth in 24 hrs.
AUGUST 5	
200 liters.....	5.0mm
300 liters.....	6.5
300 liters + sand.....	6.0
Distilled water.....	11.5
AUGUST 7	
100 liters.....	1.0mm
100 liters + sand.....	2.0
150 liters.....	2.0
150 liters + sand.....	2.0
Distilled water.....	10.0

An inspection of the results shows no apparent amelioration resulting from the presence of the solid. It should be noted, however, in passing, that compared with the electrolytes used, phenol is a weakly toxic substance, and the plants are apt to make a good growth in solutions containing a comparatively great number of molecules (9).

TABLE V.  
RESORCINOL.

1 gram-molecule	Growth in 24 hrs.
AUGUST 5	
200 liters.....	13.0mm
200 liters + sand.....	10.0
300 liters.....	10.0
400 liters.....	10.0
Distilled water.....	11.5
AUGUST 7	
100 liters.....	2.0
100 liters + sand.....	3.0
150 liters.....	3.0
150 liters + sand.....	5.0
Distilled water.....	10.0

In this substance, in concentrations great enough to interfere greatly with the growth rate, the presence of the solid seems to bring about a slightly increased rate of growth, this effect ceasing as the dilution is increased. Here we meet again a compound which is tolerated in considerable concentration by the plant (9).

TABLE VI.  
THYMOL.

1 gram-molecule	Growth in 24 hrs.	Growth in 48 hrs.
JULY 30		
2600 liters.....	0.0mm	0.0mm dead
2800 liters.....	4.0	9.0mm; 2 dead
2800 liters + glass.....	14.0	28.0mm
JULY 31		
2600 liters.....	3.5	2 dead
2600 liters + sand.....	3.0	3 dead
AUGUST 5		
2600 liters.....	2.0	
2600 liters + sand.....	1.0	
2800 liters.....	4.0	
2800 liters + sand.....	5.0	
Distilled water.....	11.5	
AUGUST 7		
2600 liters.....	0.5	all killed
2600 liters + sand.....	2.0	all killed
2800 liters.....	0.5	all killed
2800 liters + sand.....	7.0	3 living
Distilled water.....	10.0	

The results with thymol, while not homogeneous, indicate that in a concentration of one mol. weight in 2600 liters of solution no steady advantage accompanies the presence of the solid. When the dilution is somewhat increased, however, such an advantage appears. The time at our disposal was too brief to carry out the study of this compound or others as far as seems desirable. Nevertheless, the preponderance of evidence seems to indicate in thymol, and less clearly in resorcinol, a favoring effect accompanying the presence of the solid (9).

#### DISCUSSION OF RESULTS.

The general situation developed by the results detailed above may with profit be summarized in order to furnish a clear view of the facts which are to underlie our further consideration.

It appears in general that the presence of a considerable body of certain insoluble substances in solutions of strongly toxic compounds, both organic and inorganic in their nature, be they electrolytes or not, tends to decrease the toxic activity of the solutions in question.

On the whole this ameliorating action is more clearly marked in case the poisonous solutions concerned are dilute solutions of strong poisons than when relatively concentrated solutions of weaker poisons are concerned.

In general, filter paper and potato starch grains exert a more marked modifying action than dense sand, glass, and paraffin.

A number of questions immediately arise concerning the relation in which the active ions or molecules stand to this phenomenon. It seems probable that no electrical phenomena are here necessarily concerned. In the case of electrolytes such a situation might be possible, but in thymol and resorcinol we have to do with electrically neutral bodies.

A more satisfactory explanation seems to lie in another quarter. Chemists have long known that gases form a denser layer over the surfaces of the walls of containing vessels than in the free space away from the walls. Certain solids have the capacity of condensing on their surfaces larger volumes of gases than others, seeming to have specific properties in this direction. For example, platinum in a finely divided form condenses many times its own volume of oxygen. A similar phenomenon has long been known in a practical way in the case of solutions. Many years ago it was noted that bone charcoal has the property of taking certain coloring bodies out of syrups, thereby clarifying the latter products. The investigation of this and similar phenomena has shown that molecules of many dissolved substances are attracted to the surface of charcoal, quartz, and filter paper, when these bodies are placed in these solutions, and in general the greater the state of subdivision to which these insoluble bodies are reduced, the more clearly may this condensation of molecules from the solution be seen. This process by which a layer of greater molecular density is formed on the surfaces of solids immersed in solutions has been denominated by DuBois-Reymond *adsorption* (6).

Not all solids have been found to be equally effective as adsorbing

bodies and all molecules do not seem to lend themselves with equal readiness to the adsorbing influence of solids (6).

Applying this doctrine of adsorption to the results observed in our experiments, we find most points noted capable of explanation. The earlier experiments of NÄGELI (2) with *Spirogyra* in distilled water obtained from copper containers and in other solutions containing extremely minute quantities of heavy metals seem capable of satisfactory explanation. He observed that distilled water containing minute traces of metal could be rendered harmless by placing a quantity of some finely divided insoluble substance in the water. He used paraffin, graphite, filter paper, glass, and other substances, finding that they interfered with the toxic action of the metals present. Doubtless the quantity of harmful ions or molecules adsorbed was so great as to reduce the number of ions or molecules in the free body of the solution below the harmful concentration.

In the case of our lupines this same sort of action is also probably at the bottom of the ameliorating influence seen to attend the mere presence of a finely divided solid in solutions or strongly toxic agents. By drawing a portion of the ions or molecules of the poisonous substance from the free body of the solution and by retaining these molecules or ions in a molecularly denser layer over their surfaces, the solids have removed from the free solutions enough of the toxic substance to decrease its poisonous properties. Since in the case of all of the insoluble substances used, paraffin excepted, the specific gravity is greater than that of water; the solids sink to the bottom of the culture vessel. As adsorption takes place, a somewhat gradual process (6), molecules and ions are renewed from the solution above, leaving it actually less concentrated than would be the case were the solutions not provided with the solid. As a result, when the roots of the test plant are introduced into the solution, it is found to have a decreased poisonous action.

In the case of certain of the solids used in these experiments, it seems not at all impossible that a small degree of solution may have taken place. In experiments with crushed Bohemian glass this was doubtless the case, since it has been repeatedly demonstrated that such glass undergoes a slight solution even in cold water. Unfortunately we were not able to make conductivity determinations to check up this factor.

In the case of the starch grains, the potato tubers were crushed in a mortar, care being taken not to grind the material and crush the grains. The starch that settled out on washing was repeatedly washed with distilled water. Distilled water in which the starch grains were allowed to stand gave no trace of the starch reaction with iodine, a reaction which appears in case any considerable number of grains are crushed, exposing the more soluble interior layers. Some hesitation, however, may be felt as to the insolubility of the grains.

The question suggests itself as to whether all insoluble solids exert a like adsorptive action under these conditions (6). No attempt was here made to test this question, since it was not practicable under the conditions of experiment given to work with the accuracy necessary in such a study. Furthermore, since adsorption is dependent to a considerable degree on the amount of surface offered by the solid, some way of taking account of this factor would seem necessary. In the case of sand this could be done, but to carry over these values to filter paper and starch grains, consisting of masses of organic substance supposed by some (7) to have a submicroscopically porous structure, seemed to be impracticable. The lack, therefore, of any practicable unit, whether of weight or surface, by which to compare the solid substances used, made it best to content ourselves with a rough qualitative method.

In general, the most marked results seemed to follow when filter paper or starch grains were used. Whether this is due to the porous structure and consequently immensely enlarged surface, cannot here be discussed.

Another point of interest in this connection concerns the nature of the contact between the solution and the solid body. In all cases except that of paraffin the solution is capable of wetting the surface of the solid, thus bringing the molecules of solute and solvent into closest relation with the adsorbing surface. In the case of paraffin the situation is different. The solution is not capable of wetting the paraffin even when in as close contact as can be obtained. As a result, a surface of quite another sort is formed, more nearly comparable in some ways to that bounding the surface of the solution where it comes in contact with the air. At the point of contact

between the solution and the paraffin, the condition of the solution more nearly resembles the surface film. In this case this film surrounds the particles of submerged paraffin, and any properties found to be possessed by the surface of contact with the paraffin should be in a manner similar to those of surface films. However this may be, the surface of contact with the paraffin seems to be such as to bring about a condensation of molecules with a consequent removal of a portion of the poisonous substance from the free solution and a decrease of the poisonous properties of the solution. This happens, also, in the face of the fact that the paraffin floats and must condense the molecules in the upper part of the culture vessel. It might seem, therefore, that the surface portions of the solution should be markedly more toxic than the lower free portion. If this be so, the ions or molecules seem to be held so firmly by the adsorptive force that they are still in effect removed from the solution so far as the roots are concerned.

AMOUNTS OF TOXIC SUBSTANCE REMOVED FROM THE FREE SOLUTION  
BY ADSORPTION.

The results seen in the tables above given seem to show that solid bodies are capable of adsorbing molecules or ions of toxic compounds, holding them so closely that in effect they are removed from the solution. We see many cases in which the growth rate is so far accelerated by the presence of the adsorbing solid as to lead one to infer that a very considerable portion of the toxic agent may be adsorbed. In cases it is observed that reduction has so far taken place as to practically relieve the solution of its toxic properties. In some instances the solution, decidedly toxic without the solid, becomes capable of supporting a more than normal growth in the presence of the solid. Here, an abnormal acceleration replaces a marked retardation, judged from the growth rate made in the distilled water check culture. Such instances are seen in mercuric chlorid,  $\frac{m}{20,000}$ . A retardation is seen in the culture lacking the solid amounting to an average of 2 <sup>mm</sup>. When sand is added, the acceleration is so great as to bring the average growth rate in twenty-four hours to 16 <sup>mm</sup>, 4 <sup>mm</sup> more than in the control culture. In the case of silver nitrate a number of instances of this sort occur. In

case the solution without the solid permits a growth rate above that seen in the control, this increase is sometimes still further augmented by the presence of sand. The results with copper sulfate show a number of instances illustrating these different phases of action.

It is a well established fact of general physiology that many compounds which at certain concentrations act as harmful agents and depress activity become in more dilute solutions accelerators of activity. If dilution be carried on there arrives a point at which all effect ceases, and only the effect of the solvent appears. This has been pointed out by COUPIN (8) for certain salts. We may represent

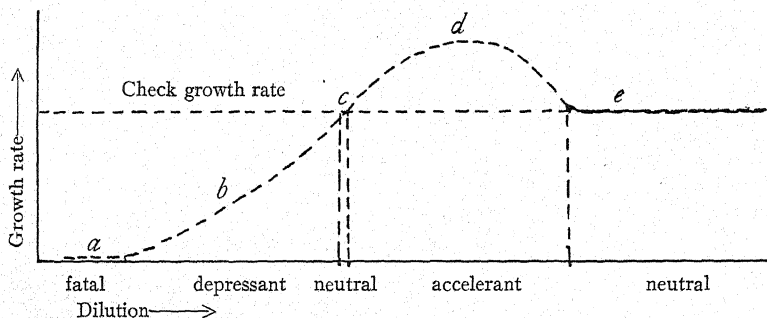


FIG. 1.

the different physiological phases resulting from the progressive dilution of a fatal concentration by a series of terms something like the following. Almost instant death (*a*) is followed by a lengthening period of survival (*b*) with depressed activity when compared with the control in water. This depressant phase is followed by a short phase in which the growth rate approximates the control (*c*). This passes over into the more extended acceleration phase (*d*) marked by activity beyond that seen in the control. This acceleration rises to a maximum and with further dilution falls off, until the solution becomes practically distilled water in its action on the organism (*e*). This may be represented diagrammatically as above (*fig. 1*), growth for the twenty-four hours in this case being indicated on the axis of ordinates, progressive dilution (that is, the degree of dilution) on the axis of abscissas progressing to the right, the growth of controls in distilled water being regarded as unaffected by other external conditions, and the roots used assumed to be in the same phase of

development. While it may not be practicable in all cases to work out all features of this generalized scheme with the very toxic salts tested, the most striking points hold.

It is now not difficult to understand a number of phenomena seen in results presented above. By preliminary tests not here detailed a concentration of each substance was found which practically suppressed growth and gave a physiological starting point from which to follow out the action of the poison along the line of progressive dilution and also in the presence of solids. In most cases, the solutions of the toxic compounds lie in the degree of concentration marked by a depressant phase of physiological action. As molecules or ions are removed by adsorption, the effect is virtually one of dilution, and the depressant action becomes less marked; or when adsorption removes a sufficient portion of molecules or ions to bring the solution into the accelerant phase, instead of the depressant, an acceleration above the control rate appears. The degree of acceleration depends on whether adsorption withdraws such a proportion of the molecules or ions as will leave the solution in its maximum accelerant phase or above or below this. It should also be borne in mind that at least theoretically, after the depressant phase has been passed, two quite differing concentrations lying on either side of the maximum may give the same physiological result. Experiments with solutions further diluted will enable one to decide on which side of the maximum the result may lie. Theoretically, a careful study of a long series of slightly differing concentrations should enable us to ascertain relatively how much of a given poison is removed by a given quantity of an adsorbing agent. This can hardly be attempted with justice from the results at hand, since they were obtained under conditions rendering the necessary accuracy of experimentation impossible. Nevertheless, I believe some rough idea may be obtained from the work presented. It will suffice to point out a few instances, since it is manifestly impossible to point out the application of this scheme to all of the results obtained.

In the case of the mercuric chlorid (p. 5)  $\frac{m}{18,000}$  is manifestly low in the depressant phase of its action, the introduction of the sand carrying it a manifest step upward, though leaving the situation



still in the depressant phase. A solution  $\frac{m}{20,000}$  permits a growth rate of  $10^{mm}$ , still less than the control having a rate of  $12^{mm}$ . The depressant phase of dilution is still represented, but is nevertheless but little below the neutral point.

The addition of an adsorbing body therefore should carry it into the accelerant phase. This is the result seen, and the growth of  $16^{mm}$  compared with the check seems to represent a rate probably near the maximum. By making a series of experiments under conditions like those met in this experiment, in which a graded series of solutions of mercuric chlorid alone is used, we should be in possession of a calibrated standard by means of which we could estimate more or less accurately the amount of the toxic molecules adsorbed. Similar methods of interpretation applied to the results with silver nitrate indicate with varying degrees of clearness a similar situation.

The results obtained with copper sulfate illustrate many of the different phases of action. In some cases the presence of the solid served not only to clearly decrease the harmful action of the salt, but even to make survival possible in concentrations otherwise promptly fatal.

In this connection a series of experiments was made to ascertain approximately in how far the quantity of solid substance present might influence the action of a toxic concentration of a salt. For this purpose a series of six cultures was prepared with like quantities of copper sulfate. To five of them prepared sand was added in different quantities. The growth rates seen in Table III, August 10 (p. 7), have been plotted in the following diagram (*fig. 2*). The growth rate in millimeters is indicated as before on the axis of ordinates. The progressive addition of solids is shown on the axis of abscissas. Although, unfortunately, no control culture was made in this case, we may fairly accept  $12^{mm}$  as average growth in distilled water on the date concerned. This value is plotted as the control result. The copper sulfate solution furnishing a basis for this experiment is concentrated enough to kill the roots promptly, usually permitting little growth. The addition of  $40^{gm}$  of sand adsorbs a sufficient amount of copper sulfate to permit half the amount of growth expected of the control culture, and in addition to make possible the survival of the test objects. Nevertheless, a sufficient concentration is still present to leave the solution in the

depressant phase of concentration. The doubling of the amount of sand brings the growth rate nearly to the normal rate of the control, a slight depressant action still being seen. The roots, however, survive in good condition, so far as their appearance indicates. The increase of the sand to 120<sup>gm</sup> results in so advanced a degree of adsorption that the growth rate is thrown clearly into the acceleration stage, perhaps near the maximum. Further additions still further reduce the molecules in the free solution and show a stage of dilution

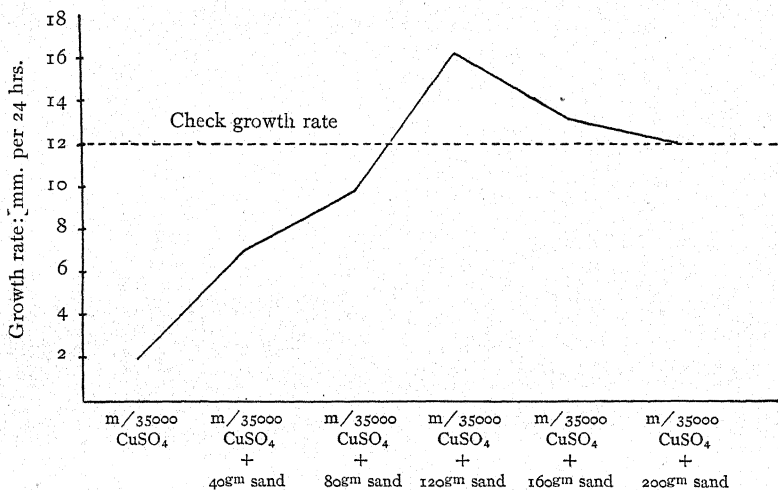


FIG. 2.

corresponding to the descending stimulus phase. The addition of 200<sup>gm</sup> of sand shows this reduction of the copper effect at its limit. The free solution is, physiologically, distilled water, so far as the duration of the experiment allows one to judge. Here then the progressive addition of quantities of a solid produces results paralleling the progressive dilution of the toxic medium, the underlying cause of these results being the gradual removal of molecules or ions from the free solution by the insoluble body present.

In view of the evidence here presented and discussed, it is likely that the process recognized as adsorption plays an important rôle in many problems of plant and probably of animal physiology. Experiments by the water culture method cannot be used as a safe basis for argument concerning soil conditions. The so-called absorptive

properties of the soil toward chemical compounds which form a demonstration experiment in the usual elementary course in plant physiology is in considerable part a demonstration of adsorption. Indeed, the whole relation of the plant to its soil environment is very largely influenced by this factor.

It is also probable that in the internal processes of the plant and of the animal, similar forces are in operation, influencing, together with diffusion and osmosis, the movements and distribution of molecules and ions within the organism. For example, it would appear not at all improbable that in cells containing starch grains or other undissolved substances, the distribution of the various molecules and ions of the cell sap is to no insignificant degree influenced by adsorption, and the transfer of molecules or ions from place to place may be modified by this tendency of the walls, starch grains, and other porous but insoluble substances to attach to themselves condensed layers of molecules or ions. Indeed, it would be easy to see in a speculative way many directions in which the processes of life may be affected by the form of activity demonstrated in the above experiments to be in operation under certain common conditions.

In nature the roots themselves and other absorbing organs furnish surfaces for adsorption and the layer of solution about them is molecularly more dense than the free solution. This applies in a much greater degree to minute, submerged forms of life, as bacteria. Absorption into the cell takes place, therefore, in general from a denser layer at the surface of the organism by the continued operation of the energy of adsorption. This surface layer is continually renewed, resulting in an accelerated absorption.

Another relation of importance is seen in the size of the organism. The more minute, the greater would be the efficiency of adsorptive activity. This may aid in accounting for the extreme efficiency of the minuter forms of life in operating on their medium.

Many suggestions occur as to divers other ways in which adsorption may play a part more or less significant in the lives of living things, but to give them value the accumulation of more evidence is necessary. Further studies in this direction are in progress.

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THE RELATION OF SOILS TO NATURAL VEGETATION  
IN ROSCOMMON AND CRAWFORD COUNTIES,  
MICHIGAN.<sup>1</sup>

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY.  
LXVI.

BURTON EDWARD LIVINGSTON.

(WITH MAP)

IN a study<sup>2</sup> of the distribution of vegetation in Kent county, Michigan, made by the author several years ago, the tentative conclusion was reached that the controlling factor in the distribution of the plant societies on the upland is the amount of water in the soil, and that this in turn is determined by two conditions, the nearness of the underground water level to the surface and the water-retaining or capillary power of the surface layers. This last factor is dependent largely upon the size of the soil particles. It was thought well to continue this subject farther north, using the same methods. Accordingly in the summer of 1902 the work here reported was accomplished. It covers nearly all of Roscommon county and the southern half of Crawford county.

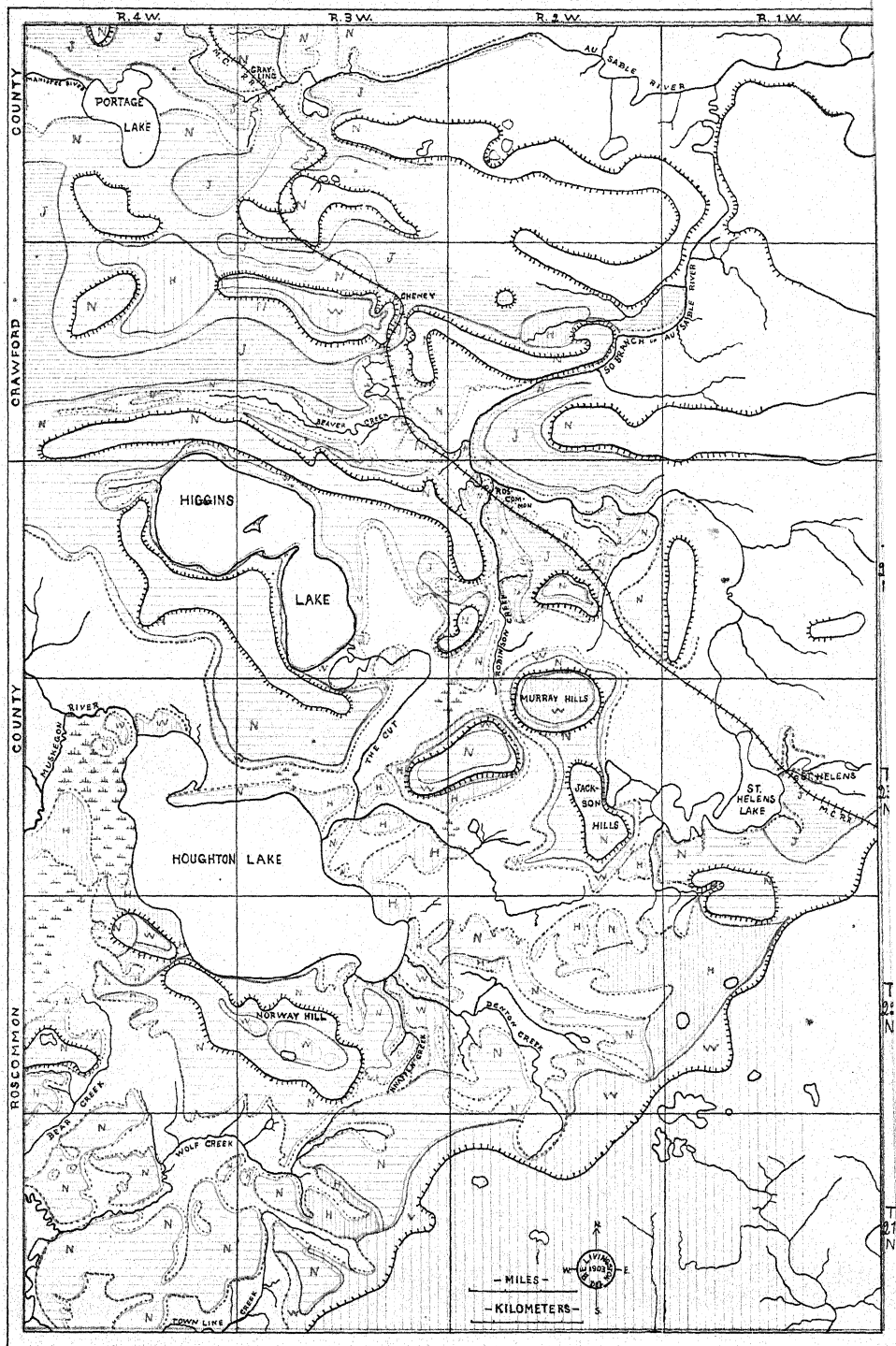
TOPOGRAPHY AND SOILS.

The region consists of a series of ridges and depressions. The former are sometimes several miles wide but more often narrow; they are always comparatively low, seldom rising more than 50 to 60 m above the level of Higgins Lake, which lies in the middle of the

<sup>1</sup> Published by permission of the U. S. Bureau of Forestry and of the Michigan Board of Geological Survey. A more detailed account of the investigations here recorded will appear in the Annual Report of the Michigan State Geologist, 1903. The map here presented is from the last-named report. A very brief statement of the conditions in this region has been published in the Report of the Michigan Forestry Commission, 1902.

<sup>2</sup> LIVINGSTON, B. E., The distribution of the plant societies of Kent county, Michigan, Ann. Report Mich. State Board Geol. Survey 1901: 81-103.

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LIVINGSTON ON SOILS AND VEGETATION.

Moraine margin .....

Clay .....



area. These ridges are moraines and between them are lower and more level stretches consisting for the most part of plains which slope downward from the ridge margin to the nearest stream. The surface soil of these plains is almost pure sand in many instances, while in others it contains enough more finely divided material to be termed loamy sand. Gravel deposits are very rare and it is seldom that one finds in the plains even scattering pebbles. The moraines are more heterogeneous in composition, containing clay, loam, and gravel as well as sand. An accurate description of these features is to be found in the geological report referred to, and will be here omitted. (See map.)

The soils are nearly all sandy, the only exception to this statement being a few low clay areas and certain clayey portions of the larger moraines. The surface soil of most of the ridges is gravelly and loamy sand, the predominating sand containing a sufficient admixture of finer particles to produce a marked difference in physical properties from that of the true sand plains, while they also contain pebbles and sometimes scattered boulders. The slopes downward from these ridges are of sand, either pure or loamy, seldom containing many pebbles of any considerable size. The true sand plains, which lie at the bottom of some of the valleys, contain little or no loamy material and no pebbles. Their surface is a fine grayish-white sand, which drifts readily by the wind when loosened. Obviously difference in degree of water-washing determines these different soil characters.

Sandy soils are composed of coarse particles and contain much silica, loamy soils are of finer particles and contain considerable quantities of alumina, while clay soils are of still more finely divided materials and contain a much larger percentage of alumina. Since all of this material was transported from the north by the glacial ice, and since it must have been quite thoroughly mixed by this agency, it is reasonable to suppose that, had it not been washed by water during and after its deposit, it would be at least fairly uniform in its mineral constituents. The washing process sorted the soils according to size of particles, but also according to their chemical nature. This is partly due to the fact that alumina breaks down into fine particles more readily than does silica. It is also due to the



fact that in well-washed soils even the less soluble constituents are apt to be actually dissolved and washed out to a greater or less degree. Thus, phosphates and sulfates are less abundant in well-washed soils than in those less thoroughly washed.

In this glaciated region, fine soils, such as clay, were either deposited under the ice of the glacial epoch, and hence not well washed, or else they were deposited from deep and very slowly flowing water. The former variety usually contains many coarser particles, as loam, sand, and pebbles. In the case of loamy soils a good part of the fine material has been washed out, but a considerable amount remains with the sand, so as to give it its loamy character; this is especially true of the ridges. Sandy soils are still more thoroughly washed; the gravel was left farther up stream, on the sides of the ridges usually, while the clay was held in suspension to be deposited at a lower level, where the velocity decreased.

On account of the difference in size of particles, which results from water washing, there naturally follows a corresponding difference in the size of the interstitial spaces of the soil; the finer the component particles, the smaller must be the spaces between them. And because of this there comes to be a corresponding difference in water-holding power and water-lifting power. The surface tension of water films is greater and hence more effective over small surfaces than over large ones, and the film surfaces are greater in coarse than in fine soil. Thus, the smaller the particles of any soil the more water it can hold and the higher it can lift this liquid from a lower level. WARMING<sup>3</sup> quotes WOLLNY as having shown that quartz sand consisting of grains over 1 to 2<sup>mm</sup> in diameter can hold only one-tenth as much water as that with grains 0.01 to 0.07<sup>mm</sup> in diameter. SCHIMPER<sup>4</sup> states that loose sand has a water capacity of 15.7 per cent. of its volume, while clay exhibits this property to the extent of 40.9 per cent.

The nature of the soil particles themselves often plays an important part in determining the water-retaining and water-lifting power.

<sup>3</sup> WARMING, E., *Lehrbuch der ökologischen Pflanzengeographie*, übersetzt von Dr. E. Knoblauch. Bearbeitet von P. Graebner. Berlin. 1902. p. 55.

<sup>4</sup> SCHIMPER, A. F. W., *Pflanzengeographie auf physiologischer Grundlage*. Jena. 1898. p. 94.

Especially is this true in the case of humus, which is composed of organic débris, decayed plant parts, and to some extent of animal offal. Pure humus has a great power to hold and lift water. This is partly because of its very fine particles, but is also to be traced in part to the actual penetration (by imbibition) of the liquid into the intermolecular spaces of the organic substance itself. Thus, by admixture of humus to a coarse (and therefore porous and permeable) soil, the water capacity of such a soil is increased. The filtering power or permeability to water of a soil increases of course with decrease in its capillary power. Also its permeability to air increases in the same way.

A general exposition of this question of size of particles, water-retaining power, etc., is to be found in either of the works just cited. A much better treatment, however, has appeared in the publications of BRIGGS<sup>5</sup> and WHITNEY.<sup>6</sup> The reader is referred especially to the writings of the former author.

Chemical analyses of a number of Michigan soils have been made and published by KEDZIE.<sup>7</sup> Table I, showing chemical constituents and water capacity, is compiled from his pages, the samples described being all from the portion of the state in which the present studies were made. The first column gives the chemicals found in the soil, in per cent. of dry weight, excepting in the case of water capacity, which is presumably given in per cent. of total volume—although this is not stated in the original papers. The upper tier gives the kind of soil, the location, and the nature of the forest cover.

<sup>5</sup> BRIGGS, L. J., *The mechanics of soil moisture*. U. S. Dept. Agric., Div. Soils, Bull. 10. 1897.

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<sup>6</sup> WHITNEY, M., *The Division of Soils*. Yearbook U. S. Dept. Agric. 1897. pp. 120-125.

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Also see WHITNEY, M., and CAMERON, F. K., *The chemistry of the soil as related to crop-production*. U. S. Dept. Agric. Bull. 22. 1903.

<sup>7</sup> KEDZIE, R. C., *The jack pine plains*. Mich. Agric. Exp. Sta., Bull. 37. Also, 27th Ann. Rept. Secy. State Bd. Agric. 1888. pp. 207-210.

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TABLE I.  
SHOWING RESULTS OF ANALYSES OF SOILS OF NORTHERN MICHIGAN.

PHYSICAL DESCRIPTION	LOCATION	Tittabawassee Valley	Mecosta co.	Gaylord	Missaukee co.	Lake co.	Average, 6 samples, Crawford and Oscoda cos.
	NATURE OF SOIL	Clay	Loam	Loam	Loam	Sand	Sand
	WATER CAPACITY	51.40	45.40	39.60	39.10	35.30	33.00
CHEMICAL DESCRIPTION	FOREST TYPE	Hardwood	White pine	Hardwood	Hardwood	Jack pine	Jack pine
	Silica.....	67.20	75.54	91.52	69.39	92.48	94.22
	Alumina.....	6.31	10.62	2.93	8.35	2.22	.....
	Fe.....	7.91	3.80	0.90	5.80	1.59	1.88
	Ca.....	1.64	0.94	0.40	1.15	0.35	0.37
	Mg.....	1.23	0.48	0.13	0.98	0.30	0.06
	K.....	1.85	1.96	0.61	1.95	0.73	0.85
	Na.....	1.15	1.25	0.28	1.15	0.32	0.27
	H <sub>2</sub> SO <sub>4</sub> .....	0.30	0.26	0.10	0.25	0.06	0.01
	H <sub>3</sub> PO <sub>4</sub> .....	0.49	0.44	0.14	0.28	0.14	0.08
	Organic materials ...	7.48	2.97	2.20	4.73	1.22	2.16

It will be noticed in the table that sandy soils usually exhibit a marked scarcity of soluble salts. This fact is perhaps to be explained by the "leaching" action of the percolating waters, as well as by the thorough washing to which these soils were subjected at the time of their deposition. The water of precipitation percolates rapidly through these porous soils and may often wash the soluble salts down toward the level of the ground water, this process being termed "leaching."

In humus-covered soils, it is probably not to the point to determine humus content and water capacity after the humus has been mixed with the loamy layers; the effect of the organic substance is very much more marked when the humus lies as a distinct layer on the surface than when it is distributed through the underlying soil. The humus layer acts like a sponge filled with water, and allows the water to pass slowly down into the underlying layers, and thus keeps them moist much longer than they would otherwise be. The samples described above probably were taken from surface soil, perhaps reaching a depth of 20 to 30 cm; nothing is said regarding this question in the reports from which these data are derived.

Table II presents the water capacity of several soil samples col-

lected by the author in Roscommon and Crawford counties. The determinations were made in this laboratory. By "surface" is meant the first 5 to 6<sup>cm</sup>, by "subsoil" the next 15 to 20<sup>cm</sup>.

TABLE II.  
SHOWING THE WATER CAPACITY OF ROSCOMMON AND CRAWFORD SOILS.

Sample No.	Township	Soil type	Topography type	Forest type	WATER CAPACITY VOLUME PER CENT.	
					Subsoil	Surface
1	21.4	Clay loam	Plain	Hardwood	43.5	74.1 humus
2	22.4	Clay loam	Ridge	Norway	45.9	40.0
3	25.4	Sand	Plain	Jack	37.0	38.0
4	22.4	Loamy sand	Plain	Norway	43.5	...
5	22.4	Clay	Plain	Hardwood	56.9	Mainly humus

It is noticeable that the subsoil of *sample 1* has the same water capacity as that of *sample 4*, but the surface humus of the former brings its water-retaining power up to a point far above that of the latter. The surface of *sample 4* was apparently like the subsoil, containing very little humus.

#### TYPES OF VEGETATION.

The vegetation of the region may be subdivided into several types or plant societies. These grade more or less into one another, but there are a few places where an observer would be puzzled to determine any particular type. There are to be distinguished four types on the upland and three on the lowland. Practically all of the area under discussion has been lumbered. A virgin pine forest is almost entirely unknown now, though some of the finest pines of the state were cut from here. The hardwood areas have been left almost untouched, excepting for the removal of the white pine originally scattered through them in many places. The hardwood is now being rapidly removed, however, and it will not be long before there will be none left. In the lowlands, the merchantable arbor vitae has very largely been removed, as has been also much of the spruce and even considerable quantities of the tamarack. In the present description there will be presented first a characterization of the original vegetational cover, as well as this can be determined at the present time; then will follow a description of the present conditions.

*I. Upland types.*

A. HARDWOOD TYPE. There is very little hardwood in the region studied, but it is quite typical of all northern Michigan. Areas so covered have not been so thoroughly lumbered as those covered with pine forests. The original form of this type comprised the following characteristic trees:<sup>8</sup> *Acer saccharum*, *Fagus americana*, *Tsuga canadensis*, *Ulmus americana*, *U. racemosa*, *U. fulva*, *Abies balsamea*, *Betula lutea*, some *Picea canadensis* and *P. mariana*, often scattered *Pinus Strobus* of enormous size, together with such low forms as *Rubus strigosus*, *Mitchella repens*, *Lycopodium clavatum*, *Taxus minor*, *Amelanchier canadensis*, *Lappula virginiana*, *Hedeoma pulegioides*, *Solidago caesia*, etc. *Acer*, *Fagus*, and *Tsuga* make up three-fourths of the forest, now one and now another of the three being dominant.

Lumbering has affected this type very little, excepting by removing the white pine, and in some cases the hemlock. Hardwood lumbering is now going on in the areas covered by this type; in these operations everything is being removed which is merchantable. Fires have not injured this form of forest to any extent, and the original humus usually remains.

B. WHITE PINE TYPE. This is typical pinery, often containing little besides white pine. Usually, however, there is an intermixture of Norway pine (*P. resinosa*), and often of hardwoods. The type is quite sharply distinguished from the preceding, but not nearly so well marked off from the following type, into which it grades in many places. As has been stated, there is at present hardly any of this type in the region under discussion. In lumbering all the pine was removed, and the subsequent fires have killed the young growth of this tree as well as the scattering hardwoods. Over vast stretches originally covered with white pine there are now no trees at all. They are regions of dwarfed *Quercus alba*, *Q. rubra*, *Acer rubrum*, and a number of shrubs. The oaks and maples are rarely more than twice as high as a man, are burned down every few years, and exist here only because of the fact that they sprout from the roots, which are not always killed by the fire. These scrub oaks and maples

<sup>8</sup> The nomenclature is that of BRITTON and BROWN's *Illustrated Flora*.

thus possess enormous roots which are partially dead or dying, gnarled, contorted, and deformed by frequent burning. For an interesting description of how maples, oaks, etc., are able to attain great age in this manner, and still not be over a few feet in height, the reader is referred to BEAL'S<sup>9</sup> paper on this subject, which is accompanied by convincing illustrations.

Among the lower forms occurring here may be mentioned the following: *Rhus hirta*, *Monarda fistulosa*, *Pteris aquilina*, *Gaylussacia resinosa*, *Vaccinium pennsylvanicum*, *V. canadense*, *Comptonia peregrina*, *Solidago hispida*, *Hamamelis virginiana*, etc. The ground between the blackened stumps is now thoroughly covered by densely growing sweet fern, huckleberry, and blueberry, the growth of the sweet fern being so luxuriant that the numerous prostrate logs are often entirely hidden from sight.

C. NORWAY PINE TYPE. At the time of lumbering, this type consisted mainly of the species for which it is named, but usually contained scattering white pine and more numerous though often dwarfed red and white oaks and red maples. The present aspect of this type is much the same as that of the preceding. The two oaks, red maple, and seedling Norway are the characteristic trees now. Seedling Norways are more numerous than in the preceding type, perhaps because of the greater number of seed trees here, as well as the somewhat greater ability of this species to withstand fire than that possessed by the white pine. The low plants are much the same as in the last. *Solidago caesia* of that type is replaced here by *S. juncea*; and *Lacinaria scariosa* is common here, as it was not in the other group.

D. JACK PINE TYPE. This is the most open of the series and occurs on the most sterile sands of the area. The only trees are *Pinus divaricata*, *Quercus coccinea*, *Prunus virginiana*, and seedlings of *Populus tremuloides* and *P. grandidentata*. All but the pine and oak are hardly more than shrubs. Besides the trees there occur on the jack pine areas the following low plants: *Pteris aquilina*, *Solidago nemoralis*, the three blueberries above mentioned (but rarely the huckleberry), *Arctostaphylos Uva-Ursi*, *Comptonia peregrina*, *Prunus*

<sup>9</sup> BEAL, W. J., Observations on the succession of forests in northern Michigan. 27th Ann. Rept., Bd. of Agric. Mich. 1888. pp. 74-78.

*pennsylvanica*, *P. pumila*, *Andropogon scoparius*, *A. furcatus*, *Danthonia spicata*, *Lacınaria cylindracea*, *Salix humilis*, *Cladonia rangiferina*, etc. This style comprises the worst part of what is called the "plains."

## 2. Lowland types.

For the most part the swamps which were originally wooded have not been denuded of forest. Where they contained white pine, that was taken out, leaving the other trees, which protected the undergrowth and soon produced a dense, almost jungle-like formation. Within the past few years the merchantable arbor vitae and tamarack have been removed from these swamps, but almost always enough small trees are left to produce shade. Also, the swamps have not been subjected to burning nearly so often as the uplands, and are generally in much more nearly their original condition than are the latter. The three types may be described as follows:

E. OPEN MEADOW TYPE. This is partly open hay meadow (largely of "blue-joint," *Calamagrostis canadensis*), partly of bulrush and cat-tail marsh, and partly of sphagnum bog. It grades into the other two types.

F. TAMARACK-ARBORVITAE SWAMP. This is the most typical swamp of the region. It contains *Larix laricina*, *Thuja occidentalis*, *Picea canadensis*, *P. mariana*, *Abies balsamea*, which form dense and often impassable thickets. In some localities *Larix* occupies almost all the ground to the exclusion of other trees, and in other places the same is true of *Thuja*. But there is not nearly so much tendency here for these two trees to form separate and distinct types as is found farther south.<sup>10</sup> There the tamarack seems to occupy the portions of the swamp lands which are most poorly drained, the arbor vitae growing in localities where drainage is more thorough, yet still not complete enough for the river swamp vegetation. Here the question of drainage does not appear to play so important a part.

G. MIXED SWAMP. This formation is found near swamp margins, especially where the underlying clay is near the surface. Thus it often occurs along lines where the hardwood forest reaches down

<sup>10</sup> For a description of the conditions farther south in the state, the reader is referred to the author's paper on Kent county, *loc. cit.*

toward a swamp. It may be looked upon as intermediate between the tamarack-arborvitae type and that of the hardwood. There is always a great mingling of species here. Among the trees are; *Larix laricina*, *Thuja occidentalis*, *Picea mariana*, *P. excelsa*, *Abies balsamea*, *Betula papyrifera*, *B. lutea*, *Fraxinus americana*, *Tsuga canadensis*, *Sorbus americana*, *Acer saccharum*, *Prunus serotina*, *Pinus strobus*, *Amelanchier canadensis*, etc., together with such low forms as *Rubus strigosus*, *R. villosus*, *Pteris aquilina*, *Lycopodium clavatum*, *Taxus minor*, *Alnus*, and *Ilex verticillatus*. The relative proportions of the different trees vary from one locality to another, so that nothing definite can be stated in this regard.

#### DISTRIBUTION OF FOREST TYPES.

The actual distribution of the types is shown by green lines on the accompanying map. The upland types are denoted by letters, each area bearing a letter to denote the type which it represents. Thus, *H* denotes hardwood; *W*, white pine; *N*, Norway pine; *J*, jack pine; and these letters stand for types *A*, *B*, *C*, and *D*, respectively. Of the lowland formations the open meadow is represented by the conventional sign for marsh where it exists over broad areas.

The main facts of distribution are presented in the following paragraphs. The upland and the lowland types will be considered separately.

#### *Uplands.*

The hardwood type occurs in this region always on soils which contain considerable amounts of clay. Such soils are always covered to a depth of several inches with leaf mold or humus, and in this layer the seedlings of hardwood and hemlock grow and thrive.

The white pine type occurs in the clayey Murray Hills, on the most clayey parts of Norway Hill, and on the great southeastern moraine, in T. 21 N., R. 2 W. These soils are often as clayey as those of many of the hardwood areas, but are higher and therefore better drained. It also occupies most of the gravelly ridge in T. 25 N., R. 2 W. Very often the swamp margins are occupied by this type also, especially where the slopes are not abrupt, a condition which gives humus a chance to collect in the sand.



The Norway pine type occupies gravelly ridges and loamy sand plains. The soil here is somewhat lighter than in the locations held by the last-named type, but it is generally too poor for profitable agriculture. As will be seen by a glance at the map, most of the uplands here studied were originally covered by this type.

The jack pine type occupies only the most thoroughly washed of the sand plains. The localities held by this open formation lie in the valley of the Au Sable. The parts lying about the headwaters of the Muskegon have abundant plains of loamy sand, but these support the type of Norway pine. This fact has no connection with the rivers themselves, however, for farther down the Muskegon are to be found typical jack pine barrens. The soil of the jack pine type is almost worthless for agriculture; it is light and dry, and where the surface is broken it is apt to be wind-blown, and often forms small traveling dunes.

#### *Lowlands.*

The distribution of the lowland type was not worked out with accuracy. Great difficulty was experienced in studying such areas, for the swamps are often almost utterly impassable. The greatest areas of open marsh encountered are marked on the map, as already described. There are doubtless many areas of like nature which were not seen at all, but these cannot be of very great extent. In all the swamps the ground is covered with a layer of humus, usually of the nature of peat, and there seems to be no difference in this substance between the sand and the clay areas. Neither is there any apparent difference in the swamp vegetation whether it is upon sand or clay.

#### RELATION BETWEEN DISTRIBUTION OF FOREST TYPES AND THAT OF SOIL TYPES.

The upland types seem to be very closely dependent upon the nearness of the underground water level to the surface and upon the nature of the soil. The former factor determines at once whether the vegetation shall be classified as upland or lowland. The distinction between these two classes is more evident on the surface than it is after closer study; it is difficult to state just how far the water level may recede from the surface and still support a lowland

type of the forest. Very few determinations have been made in this regard. MAYR<sup>11</sup> states for northern Wisconsin that where the water level is less than 2.5<sup>cm</sup> below the soil surface, the vegetation is of the swamp form; while if it is lower than 2.5 to 5<sup>cm</sup> the soil bears white pine or some other upland type. This was on sandy soil. WARMING<sup>12</sup> has determined the depth of water level in various soils in Denmark. He finds *Juncus* and *Carex* forms holding the ground until the water level is about 22.5<sup>cm</sup> below the surface; with water at a depth of 30 to 37.5<sup>cm</sup>, grasses grow well, forming what we should term a moist meadow. With the water from 45 to 60<sup>cm</sup> below the surface, all grains grow well; this seems to represent our fertile uplands. With the water still lower the soils becomes poor for grains. Data from natural vegetation, so far as I know, have not been gathered.

The more water there is in a soil, the less is the access of air to the roots of plants growing therein. This is because air diffuses much more slowly when in aqueous solution than when in the form of a gas. Gas diffusion is checked by the filling of the interstices of the soil with water, and hence most of the oxygen which reaches roots in wet soil must do so by diffusing as a solute in the water. Some ordinary plants cannot grow without rather free access of oxygen to their roots, and so it follows that a soil saturated with water is very poorly adapted to their growth.<sup>13</sup> This is probably the main reason why saturated soils are usually occupied by a vegetation differing entirely in aspect from that found on soils which are drier; thus we have swamp or lowland types of vegetation contrasted with upland types. Swamp plants are able to live with a scanty supply of air to their roots; but since upland plants cannot, it is possible to have too much water in the soil for the well-being of the latter. Thus areas with much water are occupied by typical swamp plants, often perhaps because they alone are able to live in this situation.

<sup>11</sup> MAYR, H., *Die Waldungen von Nordamerika*. München. 1890.

<sup>12</sup> WARMING, E., *Excursionen til Skagen i Juli 1896*. Bot. Tid. 21: 59-112. figs. 4. 1897. I am indebted to G. H. Jensen for an abstract of the article.

<sup>13</sup> WOLLNY, E., U. S. Dept. Agric. Exp. Sta. Record 4:528-543, 627-641. 1893.

1. *Factors of distribution in the uplands.*

ORIGINAL DISTRIBUTION. Throughout the uplands, excepting in the narrow swamp borders and in the low clay plains about Houghton Lake, the underground water level is far from the surface, its depth varying from 3 to 25<sup>m</sup> or even more.

Wherever the upland group occurs near the water level, it takes the form of one of two types, either the hardwood (on the low clay) or the white pine (on the low sand and loam). Farther above permanent water the former of these types occurs only in one locality, in the northwestern part of the area, and there upon loam. Where the water level is not near the surface, the white pine type occurs only on clay and loam. The Norway type is found throughout the area on loamy, or loamy and gravelly sand, and the jack pine type appears exclusively on sand which is hardly at all loamy and thoroughly washed. The distribution of the upland types just described may be tabulated as follows:

POSITION OF UNDERGROUND WATER LEVEL.

Soil	Near surface	Deep
Sand .....	B, C .....	D
Sandy loam.....	B, C .....	C
Clay loam.....	A, B .....	B (A) <sup>14</sup>
Clay.....	A, B .....	B

In the above table the different types are denoted by the letters already used in their description. It will be noticed that from clay to sand, with water level deeply seated, we have a series passing from the white pine type to that of the jack, through the Norway. A single exception to this is the hardwood area on clay loam in T. 25 N., R. 4. W, to be spoken of in a later paragraph. But with the water level near the surface, the series runs from the hardwood to the Norway type, the jack pine not occurring at all. This observation seems to agree with those made by MAYR<sup>15</sup> in northern Wisconsin. He states that sand ridges rising out of the swamps usually bear white pine on the slope, then Norway, and lastly the jack on the most elevated parts. The same author points out that white pine will grow on poor sand if the water is only near the surface. The same seems to be true here also.

<sup>14</sup> The hardwood in T. 25 N., R. 4 W.

<sup>15</sup> MAYR, H., *loc. cit.*, p. 207.

To explain the distribution of the different types, either of two hypotheses may be resorted to. As has already been mentioned, the finer the particles of the soil, the greater its power to lift and hold water above the underground level. It is well known, too, that some soils contain more of certain salts than do others. Thus, the reason for the observed distribution on the uplands may be sought for either in the water-retaining power of the soil or in its chemical constituents.<sup>16</sup> That the depth of the water table itself sometimes plays an important part in determining plant distribution is shown by the above table. Along a swamp margin the increased amount of water may influence the plant growth directly, but how much of the observed influence is to be considered as indirect is an open question. The presence of water alters a number of other soil factors.

First, it checks free access of air. Thus, if jack pine roots need more air than do those of Norway, this might explain why the former fails along the swamp borders and the latter takes its place.

Secondly, with increase in water content there follows a more equal distribution of the dissolved salts, for these can diffuse only through continuous water films, and the greater the cross-section of the latter, the more rapidly will diffusion take place. As a corollary to this statement, it follows that "leaching," the washing down of soluble salts out of the upper into the lower strata, cannot occur to any great extent in a soil which is constantly filled with water. Moreover the upward diffusion of salts during dry times would probably more than counteract the downward washing during heavy rains. The upper layers of a wet soil are apt to have more soluble salts after they have lain for a time than when first placed. This is of course on account of the evaporation at the surface, which increases the concentration of the soil solutions in the upper layers. Of course

<sup>16</sup> For early papers on this subject see:

THURMANN, J., *Essai de phytostatique appliquée à la chaîne du Jura*. Berne. 1849.

NÄGELI, C., *Sitzungsber. Akad. Wiss. München*. 1865.

UNGER, *Ueber den Einfluss des Bodens auf die Verteilung der Gewächse*. Wien. 1836.

A more recent paper dealing with this question of soil physics and soil chemistry as influencing vegetation is COWLES, H. C., *The influence of underlying rocks on the character of the vegetation*. *Bull. Amer. Bureau of Geog.* 2:1-26. 1901.

this indirect effect cannot be exhibited unless there is a sufficient amount of salts in the deeper lying soil. But in a glaciated region such as this, there can be little doubt as to the presence of these relatively near the surface.

Thirdly, the checking of air access, coincident with the filling of the pores of the soil with water, must check the process of oxidation and thus accelerate the formation of humus. This seems to be a very important factor in determining vegetation.

Fourthly, the growth of micro-organisms in the soil, bacteria, etc., takes place much more rapidly in a moist than in a dry soil. However, excess of water is deleterious to the growth of many of these organisms, so that a soil may be too wet for them; but flooding is not so fatal in sand as in finer soils.<sup>17</sup> It is well known that soil bacteria and mycorrhizal forms are very important in increasing the amount of nitrates in the soil, and thus it appears that a moist soil, even a wet soil, if it be sandy, will gain nitrates much more rapidly than a dry one.

The comparative rapidity of temperature changes in moist and dry soils may have considerable importance in regard to plant growth. A dry soil is subject to much more sudden and rapid changes of temperature than is a moist one when the soils are exactly alike, as I have shown by actual tests.

The points of difference between a moist and a wet soil may be tabulated as follows:

Condition of soil.....	Dry	Moist	Wet
Water for roots.....	Too little	Enough for most plants	More than needed for most plants
Soluble salts originally near surface.....	Sometimes leached farther down	Still near surface	Still near surface
Soluble salts originally in lower layers.....	Sometimes leached farther down	Partly in upper layers	Partly in upper layers
Humus content.....	None	Some	Plentiful
Oxygen content.....	Plentiful	Some	Little
Micro-organisms.....	None	Optimum	Few
Nitrates.....	Little	Much	Some
Temperature changes.....	Rapid	Less rapid	Slow

Whether these points are determined by nearness of the underground water level or by the capillary power of the soil, there appears to be no doubt that the amount of water in the layers near the surface practically determines the nature of the vegetation in this region. Besides the general discussion of this matter to be found in

<sup>17</sup> GAIN, E. Action de l'eau du sol sur la végétation. Rev. Gén. Bot. 7:16-26, 71-84, 123-137. 1895.

WARMING and SCHIMPER (*loc. cit.*), the reader may refer to GAIN<sup>18</sup> and HEDGCOCK.<sup>19</sup>

Of the upland series, the hardwood type of vegetation seems to need the most water, the most soluble content, and the most humus. Probably this is the reason why this type occupies the moister soils of the upland, no matter whether these are moist through nearness to the underground water table or through the lifting power of the soil itself. The types of white, Norway, and jack pines seem to require less water in the order of their arrangement. Probably the Norway and jack pines require more air in the soil than either the hardwood or the white pine. The typical tree forms of both these last-named types occur in the mixed swamp quite commonly, but I have yet to see either Norway or jack pine in soil which is wet the greater part of the year. Throughout the region it seems that each type occupies soils which correspond in water content to its needs. It must be remembered here that a sandy soil near the water level may contain much more water than a loamy one where the water is farther from the surface. This idea offers a possible explanation for the occurrence of hardwood on low loam in T. 25 N., R. 4 W. Addition of surface humus has also, perhaps, raised the water holding power of the soil to the neighborhood of that manifested by clay itself. The subsoil is such here that the white or Norway type might be expected.

PRESENT DISTRIBUTION. The statement so frequently met with that white pine will not come up after it has once been cut off and the ground burned over seems to strike wide of the truth in this region. I have visited almost every square mile of the uplands and am thoroughly convinced that scattering seedlings of white pine are now evident on practically all areas originally covered by that species, which have not been recently subjected to the action of fires. Seedlings of the Norway, however, are now more numerous on these areas than are those of the white pine itself. They are plentiful throughout the region on light soils excepting the very lightest.

<sup>18</sup> GAIN, E., *Recherches sur le rôle physiologique de l'eau dans la végétation*. Ann. Sci. Nat. Bot. VII. 20:65-215. 1894.

<sup>19</sup> HEDGCOCK, C. G., *Botanical Survey of Nebraska: Studies in the vegetation of the State*, II. Lincoln. 1902.

Fires prevent the young growth of the white pine and also prevent humus formation. Thus, as long as the latter are allowed to continue, the water capacity is not apt to rise and the growth of nitrifying bacteria is not apt to increase; but the presence of a few white pine seedlings is evidence that the species can grow if protected. Indeed the best young stands of any kind that I have seen are of this tree, and they promise exceedingly well for reforestation.

As has been said, the Norway pine is coming in quite freely in the areas originally covered by this species and the white pine. The degeneration goes no further, however; I have almost never seen even individual jack pines appearing in any of these areas. Indeed, there is some evidence that the Norway pine is gradually advancing its seedlings into the areas held by the jack pine.

The hardwood forest reappears quite rapidly when cut. This is doubtless in part due to the fact that this material does not burn so readily nor so violently as do the pines. The scattered white pines which formerly characterized some of these forests in the eyes of the lumberman are not returning. They are perhaps only a relic of a past generation of forest.<sup>20</sup> Hemlock is reproducing well and will return with the beech and maple if through lack of humus the soil does not become too dry for the seedlings. The sugar maple is the best for reclaiming cut-over lands. Its seedlings stand close together and do not seem to suffer from one another's shade.

The work of SHERRARD<sup>21</sup> in this region resulted in a map and statistical study of the tree growth of township 25 N., R. 4 W, as well as a general discussion of the forestry conditions of the reserve. The township thoroughly studied by this author originally contained practically no white pine, but the other types are well represented. SHERRARD'S "oak flat" and "oak ridge" are all original Norway pine land. For statistics of growth, etc., the reader is referred to his paper.

<sup>20</sup> See the author's Kent county paper, *loc. cit.*; also WHITFORD, H. N., The genetic development of the forests of southern Michigan. *BOT. GAZ.* 31:289-325. 1901.

<sup>21</sup> SHERRARD, T. H., The Michigan forestry reserve. Report Mich. Forestry Commission 1902: 28-54. 1903.

## 2. *Factors of distribution in the lowlands.*

The three types of lowland vegetation seem also to follow in some degree the conditions of soil moisture. In this case it seems better, however, to arrange the types in the reverse order and to present them as following conditions of drainage. As has been stated, all three types are composed of forms which can withstand a great deal of moisture. No positive evidence can be given as to whether or not there is any difference in water content between the soils of the open meadow and those of the tamarack-arborvitae forest. Nothing has been made out regarding the conditions which decide in favor of one or the other of these; but the mixed type is always found on the better drained portions, where there are hummocks raised out of the saturated soil, and where the general level is a few inches higher. Often this better drainage seems to come about merely by accumulation of vegetable debris, a fact which suggests that perhaps in time the conifer swamp might give way to the mixed, and at last possibly to the hardwood upland type.

Attention has already been called to the fact that this series of types have not been seriously altered by the hand of man. The large white pines have been taken from the mixed swamps, as have also many of the most valuable tamaracks and arbor vitae, but the forest conditions have not generally been destroyed.

### RELATION OF THE VEGETATION TO THAT OF KENT COUNTY.

The predominance of the pines in the region under discussion is an expression of the fact that the flora here is a typical northern one. Only one pine (the white) is found in Kent county, and there it grows in poorer soil than it holds here. The presence of hickory and the better growth of the black, red, and white oaks in the more southern area is an indication of a more southern flora. The factor which keeps the jack pines out of the more southern county may be a climatic one; this species occurs with the white pine on the dunes at the extreme southern end of Lake Michigan.

The hardwood forests of the two regions are very nearly the same in character. In the northern part of Kent county the hemlock begins to be an important tree in this group, as it is farther north.



A study of the transition zone between these two areas will be necessary before the working out of the exact relation of the various societies can be attempted.

#### RELATION OF THE VEGETATION TO THAT FARTHER NORTH.

The student of plant distribution who has formed any definite theories as to the relation of plant societies to topography and soils from the southern part of the state and from Indiana and Illinois will be much surprised if not actually shocked by a visit to the region of the straits of Măckinaw. On the island of Mackinac, for example, occur most of the tree forms found in Kent county, but growing apparently without relation to the soil condition. Norway and white pines, beech, sugar maple, red maple, tamarack, arbor vitae, balsam fir, basswood, etc., will be found growing side by side on the well-drained uplands in clay or sand or loam, or even partially bare rock. As to the reasons for this nothing can be said before more of the area has been studied in detail.

#### CONCLUSION.

It appears from these investigations that the main factor in determining the distribution of the forests on the uplands of this region is that of the size of soil particles, the sorting of which dates back almost entirely to the close of the last glacial epoch. The size of particles determines the amount of air and moisture in the soil, and these in turn determine the amount of humus formation and the growth of nitrifying organisms, and perhaps also to a certain extent the amount of soluble salts in the surface layers.

A factor of less importance, because applicable only over small areas, is the nearness of the underground water level to the surface. This affects the uplands only along swamp borders.

In a broad way, physiography may be said to determine the vegetational distribution here.<sup>22</sup> The physiographic features are largely ones of glacial topography or are traceable directly to these. Geological factors, in one way or another, have of course determined

<sup>22</sup> For an excellent elaboration of this idea see COWLES, H. C., The physiographic ecology of Chicago and vicinity. *BOT. GAZ.* 31:73-182. 1901. Also, The plant societies of Chicago and vicinity, *Bull. Geog. Soc. of Chicago* 2:1-76. 1901. Also, The physiographic ecology of northern Michigan, *Science N. S.* 12:708, 709. 1900.

the distribution of surface soils and the distance below the surface of the ground water level.

It is probable that many dry soils may at length become moist enough to support one of the more moisture loving types of vegetation, simply by increase of humus content, which must go on slowly at first but more rapidly as the amount increases. This is merely an application of one of the general principles of forest succession pointed out by WHITFORD (*loc. cit.*).

The lowlands are covered with a vegetation complex of species such that they can bear excess of water and paucity of oxygen in the soil. From the open meadow and coniferous swamp we pass, with better and better drainage, through the mixed swamp to the hardwood or the white pine of the uplands.

It appears that the natural reforestation of the pine areas, with Norway pine, and to some extent at least with white pine, will take place if the fires can be suppressed.

THE UNIVERSITY OF CHICAGO. \*

NOTE.—Since the preparation of this paper, a similar conclusion has been reached in regard to sterility in agricultural soils by WHITNEY and CAMERON, Bull. 22, Bureau of Soils, U. S. Dept. Agric. 1903. Also, it has been shown by actual field test that coarseness of soil particles alone can produce sterility in spite of a plentiful supply of water. See LIVINGSTON and JENSEN, An experiment on the relation of soil physics to plant growth. BOT. GAZ. 38: 67-71. 1904.

## NEW AND NOTEWORTHY WESTERN PLANTS. .II.

A. D. E. ELMER.

IN the spring and summer of 1902, while engaged in a collecting trip in western Santa Barbara, eastern Ventura, and portion of northeastern Los Angeles counties of California, a number of noteworthy plants were collected as well as new species discovered. On the train from Stanford University to Santa Barbara, where my headquarters were made, I was impressed with the surroundings of Surf as having peculiar physical characters. Having no time to examine the vegetation then, I observed nevertheless a palmlike bush with large golden yellow flowers which I did not notice farther south. Curious to know this plant, I made a side trip to Surf in May, and found its local sand-dune flora the most interesting of all the vegetation in the counties visited. Surf is near the coast and has a stretch of sand dunes a few miles in length and a half mile in width. The breakers are active most of the year, and the winds at certain seasons are continuous and strong; at such times the sands are shifting almost knee-deep. The temperature is always moderately cool. This place is one of the few points along our coast possessing more striking peculiarities than the ordinary sea beaches. It is a place where the oceanic influences are predominant. One can imagine similar conditions on the Santa Barbara Islands off the mainland of southern California. It is my conviction that if a critical study were made, comparing the island flora with that of the mainland such as we have at Surf, a striking similarity would be discovered. Of the following species, all are described as new excepting the first four, and the first seven were collected in the vicinity of Surf. Some of these seven have already been reported from the islands, and the others may be assumed to belong to the island flora.

*DITHYREA CALIFORNICA* HARV.—This peculiar crucifer I collected on the sand hills at Surf, and it was collected again in the Mohave desert at Lancaster, Los Angeles county, California. It seems to extend from the coast of southern California northeastward through the Mohave desert to Nevada. So far as I am aware, Surf is the

most northern limit of its distribution along the coast, and it may be expected on the Santa Barbara Islands.

*MESEMBRIANTHEMUM CRYSTALLINUM* Linn.—This beautiful ice plant seems to love halophytic conditions along drifting sand beaches continually swept over by cool winds from the ocean, though it has also been reported from the Mohave desert by Mrs. BRANDEGEE, according to PARISH. Along this coast its range extends from Surf, Santa Barbara county, California, southward through Lower California, and on the islands off the coast. It is an old world species, indigenous to the coast of Africa.

*LEPTOSYNE GIGANTEA* Kellg.—This is the plant observed from the moving train as a palmlike bush with large golden yellow flowers. Aside from the original publication, the *Botany of California* reports it from Guadalupe Island and San Miguel of the Santa Barbara Islands. The *Synoptical Flora* gives it from the mountains near Santa Barbara and San Miguel, and the islands off the coast. This citation is rather obscure, and it is to be doubted whether this plant was discovered on the mainland as early as that date. In Bull. Calif. Acad. 4:402. 1887, GREENE writes that he found it frequent on cliffs toward the sea on the north side of Santa Cruz Isand, and reports it flowering as early as February and March. Miss ALICE EASTWOOD reported it for the first time from the mainland, and in Zoe 4:286. 1893-4, she writes that JARED found it growing abundantly near the old wharf at Point Sal, Santa Barbara county.

*CEANOETHUS IMPRESSUS* Trel.—About twenty-four years ago JARED collected southwest of Guadalupe toward Point Sal, Santa Barbara county, California, a *Ceanothus* of which TRELEASE wrote in *Proc. Calif. Acad.* II. 1:112. 1888:

*C. impressus*, n. sp. Villous with short spreading hairs: leaves broadly elliptical to nearly orbicular, 6-8<sup>mm</sup> long, loosely villous, especially on the veins below, the upper surface deeply furrowed over the midrib and several pairs of lateral nerves, the slightly glandular margin very revolute, appearing as if crenate: peduncles about 10<sup>mm</sup> long, scaly toward the base; inflorescence subglobose, compact: fruit not seen.—Santa Barbara county, Cal.

About fifteen years later Mrs. IDA BLOCHMAN collected it again near the same place. While botanizing a few miles north of Surf station I found a *Ceanothus* (distributed under number 3870) which

seems to answer well to the above diagnosis. Its range appears to be restricted to this coast, and it should be looked for on some of the northern Santa Barbara Islands. In Proc. Calif. Acad. II. 4:202. 1894-5, Mrs. KATHERINE BRANDEGEE writes that in her opinion it appears to be nothing but a stocky southern form of *C. dentatus* T. & G. growing on unsheltered sandhills. In the same paragraph she states that *C. dentatus* in its typical form appears to be confined to the vicinity of Monterey. Still there are quite remarkable differences between the two forms or species, and to one observing them in the field they would not for one moment be taken for the same. *C. dentatus* at Monterey has not the dense prostrate habit. The leaves of *C. impressus* are broadly elliptical to nearly orbicular, while in *C. dentatus* they are oblong-cuneiform; furthermore, the branches of *C. impressus* are rigid and spinescent, while in *C. dentatus* they are flexible and not spinescent—a character also contrasting *C. thyrsiflorus* Esch. and *C. sorediatus* H. & A.

**Malacothrix succulenta**, n. sp.—Succulent maritime perennial herb, with long fleshy creeping and numerous branched stems forming dense mats: stem above the sand branching near the base or at least below the middle, 1-2<sup>cm</sup> high, rarely erect but usually reclining, when young floccose especially on the concealed portion, soon becoming glabrous: lower leaves persistent after they become dry, linear-oblongate, sessile when mature, glabrous on both sides, 5<sup>cm</sup> long, 8<sup>mm</sup> across the widest part, obtusely rounded, rarely undulate or dentate along the upper margin: scapes gradually thickened at the apex, usually branching from a little below the middle, its bracts minute, weak and sub-flexuose: heads solitary, turbinate, 2<sup>cm</sup> long, about that in width at the top: involucre bracts chiefly in one series, 10<sup>mm</sup> long, thin, glabrous, linear, loosely imbricated, subtended by numerous smaller triangular bracts of the scape: flowers many, all with lemon-colored ligulate corolla: receptacle naked, flat: achene smooth, 1.5<sup>mm</sup> long, with semi-truncate or short obtuse ends, bearing a soft silky white pappus whose bristles are finely scabrous and equally 6<sup>mm</sup> in length: corolla 7<sup>mm</sup> long, gradually tapering into the 4-toothed ligulate expansion, much exceeding the pistil, its tube 3<sup>mm</sup> long and glabrous: stamens exserted; anthers linear, united, 3<sup>mm</sup> long; filaments 5<sup>mm</sup> long, distinct, thread-like style exceeding stamens, barely cleft.

Dunes and terraces about Surf, Santa Barbara county, California, May 1902. Type specimen, no. 3639, in Herb. Stanford University.

It is now just sixty-six years since NUTTALL first discovered on an island in San Diego Bay a *Malacothrix* which Torrey and GRAY described (Fl. N. Am. 2:486. 1838-40) as *M. incana*. Fifty years later GREENE rediscovered it growing abundantly on San Miguel, the smallest and remotest of the Santa Barbara Islands; he also found it on the western extremity of Santa Cruz Island, a distance of 200 miles northwestward from its type locality. My plant from Surf is similar, but in my opinion is specifically distinct, though very closely related to *M. incana*.

*Carduus maritima*, n. sp.—Succulent maritime biennial or perennial, from strong thick tap roots: stems 1<sup>m</sup> long, much branched from the base and up to the middle, giving the plant a rounded bushy appearance; branches covered with long white appressed hairs and terminating in 1-3 heads: leaves thick, felty, densely and thickly lanate pubescent, 1-2<sup>cm</sup> long, the blade proper ovate in outline, the lower one-third abruptly narrowed, its base semi-auriculate, the entire margin irregularly and dentately lobed and beset with straight needle-pointed spines which are more numerous toward the base than on the coarse lobes of the blades: heads large, dull white, 5<sup>cm</sup> long, nearly that in width, loosely corymbose: bracts many, imbricate, nearly equal in length; the exterior ones similar to the leaves in lobation, spinescence, and pubescence; the interior ones linear-lanceolate, sharply acuminate, the lower and inner surface wholly glabrous, finely spinescent on the margins above the middle: the dense bristly hairs of the receptacle not hispid, dark brown, 12<sup>mm</sup> long: achene 6<sup>mm</sup> long, flattened, narrowly obovoid or cuneate, brown and shining, usually somewhat curved: pappus bristles interlaced with fine secondary ones except at the apex, 2<sup>cm</sup> long, dull white, attached as a whole to the apical rim of the achene: corolla tubular, 2.5<sup>cm</sup> long, segments 4<sup>mm</sup> long, the tube funnellform or slightly inflated immediately beneath the lobes: anthers united and pubescent, 7<sup>mm</sup> long: stigma barely notched.

Surf, Santa Barbara county, California, May 1902. Type specimen, no. 3631, in Herb. Stanford University.

The habitat of this species is strictly saline and most probably it can be found on the islands and possibly in other localities along the coast. I found only a few plants on the most exposed dunes, on which they formed low spreading bushes not very dissimilar to the Russian thistle. Its low succulent halophytic habit, remarkable pubescence and peculiar lobation and spinescence of its leaves readily distinguish it from all other species of this genus.

**Monardella crispa**, n. sp.—A low strongly aromatic shrub, 3<sup>dm</sup> high, the lower woody branches numerous, giving it a small dense bush-like appearance; younger branches lanate pubescent, older ones with thin coarsely and irregularly checked bark: leaves sparsely lanate pubescent, somewhat succulent, fascicled at regular intervals, more strongly punctiform on the dorsal surface, the larger ones 2–3<sup>cm</sup> long and 1<sup>cm</sup> wide, undulate or coarsely crisped along the margins below the rounded apex, oblong or narrowly oblanceolate with a long attenuate base; upper pair of leaves ovate to oblong, without the slenderly narrowed base: heads solitary upon the stems or branches or in a series of two or even three, sub-globose, 2–4<sup>cm</sup> across, upon densely woolly scapes 2–5<sup>cm</sup> long: bracts 1<sup>cm</sup> long, apex acute or rounded, thin, purplish, the 3–7 nerves conspicuously ascending, the outer surface soft pubescent, almost equaling the calyces, the exterior ones elliptic to broadly oblanceolate, the interior ones narrower and a trifle shorter: flowers 18<sup>mm</sup> long, upon pedicels 1<sup>mm</sup> long: calyx tubular, 6<sup>mm</sup> long, woolly pubescent, 14-nerved, the 5 acute teeth 1<sup>mm</sup> long: corolla 13<sup>mm</sup> long, light pink, obscurely bilabiate; upper lip broad, deeply emarginate; lower one divided into 3 ligulate segments; exterior corolla tube 4<sup>mm</sup> long, exceeding the calyx, sparsely set with fine short recurved hairs: stamens 4, spreading and much exserted: style included, bearing a short-lobed stigma.

Surf, Santa Barbara county, California, May 1902. Type specimen, no. 3965, in Herb. Stanford University.

This mint is a maritime species, and at Surf is confined to the drifting sand beaches. Without much doubt it may also be found on some of the Santa Barbara Islands where the sea influence is strong.

**Monardella robusta**, n. sp.—Faintly aromatic, tall, woody, 1–2<sup>m</sup> high, prostrate or supported by other undergrowth: stem almost scape-like below, with a few branches toward the top, covered with a thinly checked but not shredded bark; younger branches dark brown, sparsely pubescent, usually terminated by a solitary head though often bearing smaller axillary ones beneath them: leaves opposite, the larger ones 5.5<sup>cm</sup> long including the 5<sup>mm</sup> long petiole, 15<sup>mm</sup> wide, lanceolate, margins involute, coriaceous, nerves radiating from the midrib and ascending, prominent beneath, sunken above, entire or obscurely crenately toothed, puberulent or only sparsely

hirsute on dorsal surface, thickly white lanate pubescent beneath, sub-scarious; axillary leaves shorter and narrower, fascicled, without a distinct petiole: heads 2<sup>cm</sup> or more across, less than that in height, solidly flowered, nearly sessile or pedunculate; the lower bracts shorter and broader, 8<sup>mm</sup> long, broadly elliptic, acute or obtuse, ascendingly nerved mainly from the broad base, soft pubescent, especially upon outer surface: flowers short pedicellate: calyx tubular, 8<sup>mm</sup> long, 14-nerved, terminated by 5 acute teeth 1<sup>mm</sup> long: corolla at least 2<sup>cm</sup> long, its tube exceeding the calyx teeth by 4<sup>mm</sup>, scarcely bilabiate, lower segments 6<sup>mm</sup> long, exterior of exserted tubular part set with fine retrorse hairs: stamens 4, exserted: style slender, mostly included, 2-notched.

Rattle Snake Canyon, a few miles back of Santa Barbara towards the Santa Ynez Mountains, Santa Barbara county, California, August 1902; rare, and only found in dense thickets of underbrush. Type specimen, no. 3728, in Herb. Stanford University.

**Encelia actoni**, n. sp.—Shrub 1<sup>m</sup> high, moderately branched, forming rather unique individual bushes; wood soft; bark thin, smooth, grayish white, becoming finely checked and ultimately shredded: leaves not crowded, nor are the secondary ones fascicled, 3<sup>cm</sup> long, 2<sup>cm</sup> wide, ovate, acute, chiefly entire, 3-nerved at base, alternate, without stipules, cinereous pubescent, upon petioles 1<sup>cm</sup> long: heads 3<sup>cm</sup> in diameter, solitary upon long cinereously pubescent scapes barely bracteate below the middle: involucre bracts nearly of the same size, 7–10<sup>mm</sup> long, 3–5<sup>mm</sup> wide, imbricate in two or three series, hispidly pubescent and sub-glandular on the exterior, glabrous on the interior: ray flowers pubescent, tube bearing a pistil and gradually expanding into a truncate ligule 8<sup>mm</sup> long, not numerous, with a sterile achene 4<sup>mm</sup> long; ligule proper finely pubescent on the outer surface, light yellow, many-nerved; disk flowers perfect and fertile, subtended by bracts; these 10<sup>mm</sup> long, strongly enfolding the achene, with a prominent midnerve besides the 10–14 lateral nerves terminating in an acute glandular pubescent apex whose edges are fimbriate: corolla tubular, equaling the achene, lower one-fourth constricted, terminating in rather acutely thickened recurved apical segments: stamens included; filaments 1<sup>mm</sup> long; anthers 5<sup>mm</sup> long, introrse, with triangular apex, and minutely sagittate base: style 2-cleft, stigmatic only upon the upper outer side of the lobes;



achene 5<sup>mm</sup> long, much compressed, narrowly obovoid or cuneate, only the edges densely ciliate especially toward the apex.

Acton, Los Angeles county, California, June 1902. Type specimen, no. 3724, in Herb. Stanford University.

This interior species differs from the seacoast *E. californica* Nutt., and can at once be distinguished in the field by its conspicuous light grayish bark, its cinereous pubescence, its fewer and larger heads, and its individual habit.

**Chrysopsis californica**, n. sp.—Perennial, 4–6<sup>dm</sup> high, from woody base: stem long silky pubescent, fastigiate branching, terminating in a subcorymbose inflorescence: leaves more or less fascicled, sessile, often clasping, the average length 2<sup>cm</sup> and width 5<sup>mm</sup>, though often much shorter or longer, granular surface covered with dense white silky pubescence, edges becoming involute: heads 2<sup>cm</sup> broad, upon short leafy ascending peduncles: involucre bracts many, villous pubescent on exterior surface, linear or narrowly lanceolate, regularly imbricated in several series: receptacle naked: *ray flowers*: pappus 2-seriate; the upper of reddish-brown scabrous bristles 6<sup>mm</sup> long, the lower lighter colored; minutely paleaceous, only 0.5<sup>mm</sup> long: corolla 2<sup>cm</sup> long, lower half tubular, upper expanded into a semi-obovate or oblanceolate ligule which is closely and minutely 3-toothed at apex; opposite this primary ligule is usually present a secondary one which is shorter, more linear and inserted upon its throat: *disk flowers*: pappus bristles in one series, 2<sup>mm</sup> long: corolla glabrous and tubular, with rich yellow acute segments, 1.5<sup>mm</sup> long: filaments short, separate, inserted upon a short thick base: style exserted and deeply cleft, the branches triangular acuminate and stigmatic only on exterior surface; achenes apparently all fertile, 4<sup>mm</sup> long, short pubescent, slightly compressed or 4-costate.

Sandy soil near the beach, Gaviota, Santa Barbara county, California, May 1902. Type specimen, no. 4148, in Herb. Stanford University.

The plant is rare, and was collected at the same station where *Astragalus gaviotus* Elm. was discovered.

**Deinandra simplex**, n. sp.—Annual or at most biennial: stem brown, generally simple, chiefly branched toward the top, hispid pubescent; flowering branches ascending, leafy, the lower ones shortest, occasionally bearing subglomerate clusters below the terminal one: leaves ovate, lanceolate or linear-lanceolate, short hispid pubescent on both sides, more or less clasping at base, 1–5<sup>cm</sup> long, the smaller

ones entire, the larger ones remotely dentate: heads turbinate, 8<sup>mm</sup> long, upon leafy bracteate peduncles: 5 involucre bracts 6<sup>mm</sup> long, uniserial, narrowly oblanceolate, the apex sparsely hispid pubescent, acuminate: *ray flowers*: ligulate corollas rarely more than three to each head, the basal tubular part 1<sup>mm</sup> long, ovate, papillose; the expanded wing broadly obovate, 5<sup>mm</sup> long, nearly that in width, yellow, the apex bearing a narrow middle tooth: achenes without pappus, 2<sup>mm</sup> long, obovate, brown or possibly black when mature, puberulent, triquetrous, tightly enclosed by the involucre bracts; style slenderly 2-cleft, stigmatic on the edges for the entire length: *disk flowers*: the 5 disk flowers separated from the ray series by 5 united bracts: achenes short and sterile, bearing a paleaceous pappus 1.5<sup>mm</sup> long: corolla tubular, 4<sup>mm</sup> long, bearing 5 yellowish teeth: filaments half as long as anthers, separately inserted upon the corolla; anthers 2<sup>mm</sup> long, with constricted triangular apices: style cleft, the lobes entirely ciliate.

Quite plentiful in dry half sandy soil, Santa Barbara, Santa Barbara county, California, August 1902. Type specimen, no. 3839, in Herb. Stanford University.

***Machaeranthera pinosa*, n. sp.**—Densely tufted perennial, 1.5<sup>dm</sup> high: underground stems numerous branched, those above ground rather rigid, brown, with a short cinereous pubescence, usually divaricately 3-branched from a little above the middle, basal portion marked with ring-like scars caused by the early falling of the radical leaves: basal leaves dry and brittle, those above the middle of the stem 3–5<sup>cm</sup> long, linear-oblanceolate, densely cinereous pubescent on both sides, usually conduplicate above the middle, sessile though the lower half is narrow and petiole-like, minutely dentate, the teeth terminating in short and sharp-pointed hyaline spinules; upper leaves bract-like, broadest below the middle: heads turbinate, 1<sup>cm</sup> high, solitary or upon bracteate brown glandular pubescent peduncles 4<sup>cm</sup> long: involucre bracts imbricate, very unequal, mostly linear, acutely pointed, the exposed surface glandular, the inner surface straw-colored or purplish-blue: corolla of ray flowers 22<sup>mm</sup> long, tube minutely pubescent, 12<sup>mm</sup> long, gradually expanding into the rich purple-blue broadly spatulate minutely 3-toothed ligule: pappus in one series, 12<sup>mm</sup> long, scabrous, reddish-brown, very unequal: corolla of disk flowers 0.75<sup>mm</sup> long: stamens with anthers 3<sup>mm</sup> long

and short filaments: style deeply cleft, the branches straight and with the entire dorsal surface stigmatic; immature achene  $2^{\text{mm}}$  long, obovoid, finely pubescent.

Rather rare on the summit of Mt. Pinos, Ventura county, California, July 1902. Type specimen, no. 4145, in Herb. Stanford University.

This beautiful deep blue or purple-flowered *Machaeranthera*, like many other purely alpine plants, has the habit of apparently forcing its growth along crevices of rocky summits.

***Chrysothamnus corymbosus***, n. sp.—Shrubby,  $0.5-1^{\text{m}}$  high, numerously branched, forming well rounded bushes; wood dry, soft, yellowish, with thin shredded bark: leaves on second year old branches of varying lengths, much shorter than on younger twigs, usually fascicled, soft pubescent on both sides, dry and becoming recurved; those on the upper branches mostly of the same length,  $10-15^{\text{cm}}$  long, ascending, not fascicled, narrowly linear or oblanceolate, with a short sparse pubescence, the surface more or less glandular, obscurely punctiform: heads glomerated in rounded corymbs,  $2-3^{\text{cm}}$  across, at ends of branches: peduncles  $6^{\text{mm}}$  long or longer, they as well as the subtending bracts sparsely lanate pubescent, usually monocephalous: involucre bracts persistent, broad and mainly in two imbricate series; lower ones triangular, short and pubescent; upper ones  $5^{\text{mm}}$  long, nearly glabrous and almost shining, broadly linear-obtuse, with narrow hyaline margins: heads about  $7^{\text{mm}}$  high, cylindric or sub-turbinate, 10-flowered: ray flowers few,  $8^{\text{mm}}$  long including the ciliate pubescent achene  $2^{\text{mm}}$  long: pappus uniserial,  $3^{\text{mm}}$  long, finely scabrous, whitish and copious: tubular part of the corolla shorter than the expanded portion; pubescent; ligule broadly elliptic, yellow, thin, apex much folding over, bluntly toothed: style cleft: corolla of fertile disk flowers tubular,  $5^{\text{mm}}$  long, 5-segmented: filaments  $3^{\text{mm}}$  long; anthers  $2^{\text{mm}}$  long, linear, with triangularly constricted apices.

Near Lancaster, Los Angeles county, California, June 1902. Type specimen, no. 3668, in Herb. Stanford University.

During the middle or hottest part of the day this desert-loving plant gives off a very strong resinous odor.

***Horkelia Rydbergii***, n. sp.—Low prostrate perennial, forming dense mats: stems barely branching below the middle, the longer ones prostrate and ultimately erect or ascending,  $2^{\text{dm}}$  long or less,

branching above the middle and bearing few-flowered cymes: leaves clustered at the base, longer ones 6<sup>cm</sup> long, covered with a silky-velvety pubescence, usually with a petiole 2<sup>cm</sup> long; stipules 15<sup>mm</sup> long, adnate and conduplicate, the interior surface quite smooth, terminating in a lacinate pubescent segment 5<sup>mm</sup> long; those of the smaller cauline leaves broader, larger lobed, and nearly clasping the stem; leaflets of the lower leaves 8–12 pairs, densely silky pubescent on both sides, 5<sup>mm</sup> long, fully that in width, sessile, merely 3–5-pointed, the lower one or two pairs somewhat distant, those above the middle more or less crowded and diminishing in size toward the apex: inflorescence loosely cymose: flowers short or longer pedunculate, subtended by leaf-like bracts: hypanthium cup-shaped, 5<sup>mm</sup> broad and 5<sup>mm</sup> high including the teeth nearly 2<sup>mm</sup> long; calyx bracts in two series of 5 segments each, the outer shorter and narrower, the inner 3<sup>mm</sup> long and acute: stamens 10; filaments acuminate, nearly glabrous, 2<sup>mm</sup> long and slightly unequal in length, petaloid in color, flattened especially toward the base; those opposite the petals much shorter than the others which are exceeded by the longer calyx segments; anthers 1<sup>mm</sup> long, introrse and basifixed: petals alternating with the outer series of stamens, cuneate or oblong to obovate, 3–4<sup>mm</sup> long, 2<sup>mm</sup> wide, barely exceeding the longer of the calyx segments; between the base of filaments and receptacle proper a narrow dark-brown smooth circular band: receptacle ciliate, ovoid to conical: pistils smooth, numerous, sessile; style 3<sup>mm</sup> long, erect, straight, constricted or articulated to the ovary; achenes 1<sup>mm</sup> long, brown, semi-recurved.

Dry gravelly flat near Griffin's postoffice, Ventura county, California, July 1902. Type specimen, no. 3971, in Herb. Stanford University. Named in honor of P. A. RYDBERG.

*Castilleia gleasoni*, n. sp.—Perennial, 2–4<sup>dm</sup> high, from a hollow thick dwarfed woody base: stems mainly from the base, branched at the middle, obscurely ridged or striate, clothed with a soft pilose pubescence which conceals the more or less dry glandular surface; branches usually clustered from the distal ends of the abruptly terminated stems, striate, similarly pubescent and glandular, bearing erect or sub-flexuose spicate racemes 1<sup>cm</sup> long: leaves many but not crowded, all cauline and equally distributed; larger ones 4.5<sup>cm</sup> long, 12<sup>cm</sup> wide, 3–5-nerved, the pubescence on both sides concealing the

numerous fine sessile glands, the upper one-third divided into 3 lobes with the middle one usually broader and longer; smaller leaves linear to lanceolate and entire; axillary leaves few, short and inconspicuous, not fascicled: average bract 2<sup>cm</sup> long, strongly 3-nerved, divided to below the middle into 3 strap-like purple-red entire segments; these are obtuse or rounded, glandular and pubescent especially on the outer surface above the middle: calyx tubular, 15<sup>mm</sup> long, 4-nerved, glandular pubescent, the bilabiate part 5<sup>mm</sup> long, each bearing acute teeth 2<sup>mm</sup> long; galea 2<sup>cm</sup> long, slightly curved, slit half way down, apex narrowly truncate or faintly 3-toothed, exterior apical section glandular, middle part pubescent, glabrous at base; lower lip represented merely by 3 broad and short lobe vestiges: stamens 4, the two inner ones slightly shorter; filaments separate, thread-like, inserted upon the corolla tube beneath the throat; anthers approximate, included by the galea, the two cells unequal in length, united above the middle, distinct below: style slender, gradually enlarging toward the apex, exceeding the galea by 2<sup>mm</sup>, bearing a 2-lobed flattened stigma: capsule ascending, 15<sup>mm</sup> long, ovoid to lanceoloid, slightly dorsiventrally compressed, acute or acuminate.

Cliffs and in rock crevices on the summit of Mt. Gleason, near Acton, Los Angeles county, California, June 1902. Type specimen, no. 3659, in Herb. Stanford University.

This "paint-brush" or "red-hot-poker," as I have heard it called, is neither the early flowering *C. foliolosa* H. & A. of the seacoast nor the glandular southern *C. Martini* Abrams.

**Eriogonum baratum**, n. sp.—Annual, 3–5<sup>dm</sup> high, erect, mostly single: stems glaucescent, purplish at base, straight and erect, one-third the height of the plant, terete, of the same thickness throughout; branches 1–5 at a whorl, smooth and also glaucescent, ascending, ultimately widely branching, subtended by 3 acuminate smooth and coriaceous bracts 1–2<sup>mm</sup> long: leaves all radical, longer ones 3<sup>cm</sup> long, including the woolly petiole 2<sup>cm</sup> long which is perceptibly expanded at base; blade proper 1<sup>cm</sup> long, ovate to broadly elliptic or rotund, semi-cordate at base, upper surface glandular and woolly pubescent, lower deeply and densely lanate pubescent: flowers mostly axillary or terminal, always solitary upon slender purple-red drooping peduncles 1<sup>cm</sup> long: involucre glaucous, often minutely glandular, coriaceous, 2–3<sup>mm</sup> long, bearing five hyaline-margined obtuse teeth

from one-fourth to one-third the entire length of the involucre: pistillate flowers little protruding, the stalks apparently articulated,  $2.5^{\text{mm}}$  long, commonly 10, becoming deflexed, intermixed with ciliate bristles  $2^{\text{mm}}$  long: corolla  $2^{\text{mm}}$  long, white or pinkish, petals 6, in two whorls; outer broad elliptic or more or less rectangular in shape, with bases clawed; inner shorter, narrower and obovate: staminate flowers fewer, sessile or sub-sessile, intermixed or more or less in the central region, also subtended by ciliate bristles,  $1^{\text{mm}}$  long, petals smaller though similar in shape and equal in number: the 10 stamens included, upon slender filaments, bearing small yellow anthers: ovary smooth, elongated,  $2^{\text{mm}}$  long, surrounded by numerous sterile filaments; styles 3, spreading, terminated by small capitate stigmas; achene sub-terete and spindle-shaped, purplish, smooth.

These hills contain borax mines, and since this plant is strictly confined to this region it would seem that the salt is a necessary constituent for it.

On very hot barren exposed round-topped hills between Griffin's postoffice and Mt. Pinos, Ventura county, California, July 1902. Type specimen, no. 3593, in Herb. Stanford University.

**Lupinus glareosus**, n. sp.—An almost acaulescent annual,  $3\text{--}5^{\text{dm}}$  high, somewhat succulent though readily curing: stem very short, rather thick and hollow, terminated by a spicate inflorescence; branches with a soft short brownish pubescence, chiefly from the stem, the outer ones curved upward from the middle: leaves clustered at the point of branching, erect or ascending, upon finely pubescent petioles  $1\text{--}5^{\text{cm}}$  long, with broadened bases subtended by lacinate adnate stipules; leaflets 10, sessile, only sparsely pubescent on both sides, soft and fleshy, obovate, on an average  $15^{\text{mm}}$  long and  $5^{\text{mm}}$  wide, the older ones with a very peculiar dead scarious upper margin: spikes cylindrical,  $3^{\text{cm}}$  in diameter,  $10\text{--}15^{\text{cm}}$  long, erect and exceeding the leaves, upon pedunculate scapes: flowers in whorls of 5, upon short pubescent pedicels, subtended by acuminate similarly pubescent bracts which slightly exceed it: calyx cup-shaped at base, bilabiate, pubescent; lower lip rather broad,  $7^{\text{mm}}$  long, obtuse, 3-nerved; upper one thinner,  $3^{\text{mm}}$  long, notched; banner broadly elliptic,  $12^{\text{mm}}$  long, finely nerved and entirely glabrous; lateral wings equaling the length of the banner, nearly  $5^{\text{mm}}$  in width throughout, basal margins ciliate and abruptly terminating into a short narrow claw; keel at least  $12^{\text{mm}}$  long, falcate, with a constricted ring-like portion near

the base and with the margin of the aperture densely ciliate: stamens of two kinds; the 5 longer ones bearing small anthers, the shorter ones with linear anthers: style falcate, the stigmatic portion barely exceeding the keel; ovary covered with long rubiginous hairs; pod equally tapering to both ends, 1<sup>cm</sup> long, 2-seeded, silky pubescent, terminated by a persistent much recurved style; seeds subsessile, smooth, compressed.

Griffin's postoffice, Ventura county, California, July, 1902. Type specimen, no. 3588, in Herb. Stanford University.

It is wholly confined to dry gravelly soil along water courses, hence its name.

**Astragalus gaviotus**, n. sp.—An erect densely tufted perennial 3–5<sup>dm</sup> high: stems many from the woody base, branching above the middle, cinereous pubescent: lower leaves falling early, becoming recurved, 10<sup>cm</sup> long, subtended by distinct acute triangular stipules 5<sup>mm</sup> in length; leaflets extending nearly to the base, 7–15 remote and scattered pairs, 15–25<sup>mm</sup> long, 5<sup>mm</sup> wide, the rachis usually terminated by a solitary leaflet; lower ones strigulose and short-petioled, the larger and older ones broadly obtuse or truncate, linear to narrowly elliptic: racemose inflorescence 2–3<sup>cm</sup> long, terminating the rigid striate and strigulose peduncles 10<sup>cm</sup> long, barely exceeding the leaves: pedicels 5<sup>mm</sup> long, ascending, strigose, subtended by shorter long acuminate strigulose bracts: calyx inflated, cup-shaped, 3<sup>mm</sup> long, apex apiculate but often more or less toothed, barely pubescent with a mixture of black and whitish hairs: corolla, stamens, and pistils not seen: pod persistent, compressed, spreading or becoming pendent upon pubescent usually recurved pedicels 8<sup>mm</sup> long, dull or yellowish-white, 6–10<sup>mm</sup> wide, 20–28<sup>mm</sup> long, gradually and acuminately tapering to both ends though more often widest above the middle, apex terminated by a short blunt cusp, the sides obscurely but finely reticulated and under a lens only sparsely hairy, straighter along the dorsal edge; seeds commonly 6, slenderly stipitate, flattened, smooth, brown, semi-reniform, strongly reticulated.

Sandy soil not distant from the beach at Gaviota, Santa Barbara county, California, May 1902. Type specimen, no. 3759, in Herb. Stanford University.

This plant is usually referred to *A. filipes* Torr., which however has a more northern and interior range and a more slender habit of branching.

**ASTRAGALUS WHITNEYI pinosus**, n. var.—A handsomely tufted and spreading variety of the alpine species, with many branches from

a perennial root; branches as well as leaves subtended by short, concrete, and scarious bracts or stipules: leaves ascending, usually 4<sup>cm</sup> long, the lower one-fourth petiolate; leaflets glabrous or sparsely strigulose, 6–10<sup>m</sup> long, 7–9 pairs though the lower ones are much scattering, the terminal either in pairs or solitary by abortion, subsessile, mostly conduplicate in the dried specimens, linear to lanceolate to oblanceolate: racemes terminal, 2<sup>cm</sup> long, upon peduncles 4<sup>cm</sup> long: calyx subinflated, 4<sup>mm</sup> long, terminated by 5 short but narrowly sharp pointed teeth, short-pediceled, pubescence of black and whitish hairs: pod 3<sup>cm</sup> long, obovoid inflated, narrowed toward the base but not stipitate, reflexed, glabrous, reticulations prominent, beautifully mottled with a purple or reddish-violet, falling rather early.

Summit of Mt. Pinos, Ventura county, California, July 1902. Type specimen, no. 4005, in Herb. Stanford University.

This variety is chiefly distinguished from the typical form by its scarious stipules, more linear leaflets, and in not being stringulose.

HERBARIUM OF STANFORD UNIVERSITY,  
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## THE MORPHOLOGY OF MONASCUS PURPUREUS.\*

EDGAR W. OLIVE.

BARKER's account of the morphology and development of *Monascus* in the early part of 1903,<sup>1</sup> as will be remembered, was shortly afterward questioned in a contradictory paper by IKENO.<sup>2</sup> IKENO gave, in fact, a diametrically opposite interpretation of certain of the more important phenomena connected with the spore formation in this fungus, and even went so far as to assert positively that BARKER's "Samsu" fungus did not belong to the genus *Monascus*. If BARKER is right, then *Monascus* shows close resemblances to other Ascomycetes; if, on the other hand, IKENO's views are correct, the fungus is an aberrant form.

The main points of difference between these opposed views may be concisely stated as follows. BARKER maintains that sexual reproduction results in the formation of ascogenous hyphae. The ascogonium consists, according to him, of an elongated penultimate cell; while the original terminal cell, which is pushed over to one side by the growth of the enlarging ascogonium, constitutes an antheridial branch. Fusion takes place between the two, the elongated tip of the female cell functioning in this act as a kind of trichogyne. After fusion, this tip portion is cut off by a septum and its protoplasmic contents, as well as that of the antheridial branch, finally become disorganized and eventually disappear. It is the cut off penultimate cell of the ascogonial branch, called by BARKER the "central cell," which still further develops and produces the ascogenous hyphae. This central cell becomes enormously swollen and is invested at maturity almost completely by a mass of closely clasping sterile hyphae. During its enlargement and development it affords protection and nutriment to the growing ascogenous hyphae. The latter

\*This work was done under a grant from the Carnegie Institution.

<sup>1</sup> BARKER, B. T. P., The morphology and development of the ascocarp in *Monascus*. Ann. Botany 17:167-236. pls. 12-13. 1903.

<sup>2</sup> IKENO, S., Ueber die Sporenbildung und systematische stellung von *Monascus purpureus* Went. Ber. Deutsch. Bot. Gesell. 21:259-269. pl. 13. 1903.

arise, according to the evidence obtained by this author, as an outgrowth of the swelling central cell, which grows over the surface of the latter, closely applied to it, until it finally pushes in, or invaginates, the enlarged central cell. In this invaginated cavity, or little "nest," thus produced, the ascogenous hyphae are formed, whether as bud-dings of the end of the in-pushing hypha, or simply as segments of it, the author does not make clear. At any rate, growth continues until the closely entwined hyphae occupy almost the whole of the interior of the enveloping perithecium. "Asci are eventually produced from the ascogenous hyphae, and in each of them eight ascospores are produced. When the spores are ripe, the asci and ascogenous branches degenerate, the surrounding central cell having by this time lost its contents, remaining as a brown cuticularized enclosing wall. The spores are thus liberated into the cavity enclosed by this wall, and the ripe perithecium appears to be nothing more than a brown cuticularized sporangium-like structure." (*L. c.*, p. 204.)

IKENO apparently agrees with BARKER in regard to sexual reproduction in *Monascus*, although his evidence appears to be drawn from dubious sections, judging from his one drawing of the process. IKENO'S main point of dispute with BARKER lies, however, in the method of spore-formation. He asserts that there are no ascogenous hyphae in the *Monascus* which he studied, but that, on the other hand, so-called "spore mother-cells" arise by free cell formation. The cytoplasm of the ascogonium becomes, according to him, aggregated about certain nuclei, resulting in the formation of uninucleate "Cytoplasmaballen," or "spore mother-cells." According to BARKER'S account, these "spore mother-cells" are segments of a hypha, which become rounded up into asci. IKENO further notes that the "Cytoplasmaballen" become increased in number by fission, and that they may contain, at the culmination of nuclear division, a greater number of nuclei than is necessary for spore-formation, and he says that the extra ones degenerate. Usually six or eight spores are finally produced, which are, in his opinion, formed by free cells formation, leaving a small amount of epiplasm between and surrounding the spores, thus corresponding to conditions observed in the ascus. An agreement is noted in the final phenomena connected with the development of the fungus, in that in the mature spore fruit

the walls of the "spore mother-cells" become disorganized, thus setting free the spores within the perithecial wall. IKENO concludes with the assertion that WENT's classification of *Monascus* among the Hemiasci is strictly correct, and that BARKER's fungus is not a member of the genus *Monascus*, but that it is a typical Ascomycete.

Several important differences will be at once noted in these two accounts, the crucial difference being the one which concerns the origin of certain structures in the swollen ascogonial cell, or "central cell," as BARKER terms it. IKENO conceives of these structures, the "Cytoplasmaballen," as arising by free cell formation, simply by an aggregation of cytoplasm around certain nuclei; other nuclei in the ascogonium taking no part whatever in the process. BARKER, on the other hand, thinks that these deeply staining bodies are segments of one or more hyphae which have grown in from the outside of the central cell, and that the ultimate origin of these ascogenous hyphae is as outgrowths of the central cell itself, which finally turn and grow again into the cell from which they have sprung. Both assert that these bodies bear within them later the spores, and in other respects the two accounts in the main agree.

DANGEARD proposes now to assist us out of our difficulties by making BARKER's *Monascus* a new species. KUYPER,<sup>3</sup> the latest writer on the subject, accepts this suggestion, and in a study of both *M. purpureus* Went and *M. Barkeri* Dang., finds confirmation in the main of IKENO's conclusions, although he calls IKENO's "spore mother-cells" true asci. He adds, however, the additional observation that a nuclear fusion precedes the development of the young asci. *Monascus Barkeri* differs, according to his views, from *M. purpureus* in an important respect. In *M. Barkeri* he has the nuclei fusing in pairs *before* the formation of the asci, and in *M. purpureus*, *after* the asci are formed. In *M. Barkeri*, his observation agrees, therefore, with BARKER's assumption that nuclear fusion in pairs occurs in the enlarging ascogonium. KUYPER regards this fusion as analogous to the fusion in the young ascus of *M. purpureus*, but such a fusion as he describes in the latter should be referred rather to the later

<sup>3</sup> KUYPER, H. P., De peritheciumontwikkeling van *Monascus purpureus* Went en *Monascus Barkeri* Dang. Kon. Akad. van Wetenschappen, Amsterdam 13:46-294. 1 pl. 1904.

fusion which is known to occur in the young asci, whereas his fusions in *M. Barkeri* belong to the early sexual fusions, as are seen in *Pyronema* and other forms.

As BARKER and others have pointed out, the development of *Monascus* from the germination of the ascospores or the conidia up to the formation of the fructifications may be readily followed out in hanging drop cultures. Observations of living cultures of *Monascus* in hanging drops show that a fusion appears to take place between the basal cell of the antheridial branch and the tip portion of the ascogonial branch, which BARKER likens to a trichogyne. It appears likely that in some cases, at least, this fusion takes place after the cutting off of the tip of the ascogonium, although BARKER asserts that the act must take place before the wall is thrown across. The swelling up of the central cell and later an appearance which suggests the pushing in or invagination of the swollen central cell by some body which enters generally near the side on which the stalk is seen; further, the enlargement of this invaginated part until the central cell seems to be entirely displaced by it; and, finally, the appearance of vacuole-like bodies within the invaginated cavity and the final formation of spores, which adhere for a time in little groups, all may be readily traced in hanging drop cultures.

When one attempts to explain these appearances, however, by an examination of sections, one meets with many difficulties, as is evidenced by the remarkable differences obtained by the investigators above mentioned. I have seen in but few instances, in fact, a hypha-like outgrowth from the central cell, and, perhaps somewhat less rarely, the actual pushing in of a hypha-like body into the side of the central cell, thus forming the "nest," or invaginated cavity, in which the ascogenous hyphae develop. Another theory than that held by BARKER has suggested itself to the writer, which is borne out by many observations. Instead of the ascogenous hypha arising from the central cell, it may have its origin in the "trichogyne-like" end of the ascogonial branch. The following observations point to this conclusion. First, the rarity of protuberances from the central cell which are long enough to furnish absolute conviction that the outgrowth is a hyphal branch. They may as well be, as BARKER himself intimates, a bulging out of the swelling central

cell at a point where the investment formed by the covering hyphae is incomplete. Secondly, the fact that, in very thick sections, one sometimes finds that the invaginated cavity of the central cell is connected with the outside by a comparatively large, broad opening, where we might naturally expect a small, narrow one, since the ascogenous hyphae are relatively small. The large opening suggests the pushing in of a larger body, possibly the fertilized "trichogyne" cell above mentioned. Lastly, the frequency of occurrence in early stages of a comparatively large, deeply staining cell, lying to one side of the swollen central cell and not yet pressed into it, indicates that this deeply staining body is not a hypha with the origin BARKER attributes to it, but is instead the cell above mentioned. Should this prove true, then the fertilized ascogonial cell is in reality the end cell, while the enormously swollen penultimate cell performs a sort of "nurse-cell" function, ultimately becoming entirely displaced, its contents digested and absorbed, by the ascogenous hyphae developing within it.

That the structures growing within the cavity in the central cell are segments of ascogenous hyphae, I have no doubt; therein I agree perfectly with BARKER. For one may see in sections of almost every immature fructification young segments which are elongated and twisted and hypha-like, and which sometimes show evidences of dividing by fission, as is pointed out by IKENO. Later, these segments become rounded off and vacuoles appear in them; still further development results in the formation of their eight spores.

The *Monascus* species which I have used was first sent from Java some years ago by D. G. FAIRCHILD to ERWIN F. SMITH and was regarded by the latter as *M. purpureus* Went. Professor HARPER, who in turn received some material from Dr. SMITH, has turned the fungus over to me for examination. So far as I am able to judge from gross measurements, and from a careful comparison of figures, this form agrees with BARKER's description of his *Monascus*, and as well with the accounts of WENT, UYEDA, and others, so that my opinion is that IKENO and BARKER worked with similar forms. I find therefore in the main a confirmation of the conclusions of BARKER, as well as satisfactory explanations of the misinterpretations of IKENO.

MADISON, Wis.

## BRIEFER ARTICLES.

### FERTILIZATION IN THE SAPROLEGNIALES.

TROW<sup>1</sup> has reaffirmed his conviction that a sexual act is present in the water molds. His paper gives in detail the results of an investigation of *Achlya DeBaryana* and *A. polyandra* in comparison with my own study of oogenesis in *Saprolegnia*.<sup>2</sup> Much of his paper is devoted to a defense of his earlier work and to sharp criticisms of the skepticism of myself and others.

*A priori* there is of course no reason why the Saprolegniales should not show examples of sexuality; the discussion has only been on the evidence that TROW presented in his paper of 1899.<sup>3</sup> This evidence consisted in the varying number of nuclei present in the oosphere and oospore, expressed by TROW in the ratio 1:2:1, and certain figures of male gamete nuclei within the egg which did not seem to me clear enough to be convincing and appeared capable of other interpretations. I found that binucleate eggs, young and old, were "quite common" in an apandrous form of *Saprolegnia mixta*, and that by the methods of oogenesis bi- and trinucleate eggs might be expected in any of the Saprolegniales. Indeed all investigators of this group, HUMPHREY, HARTOG, and TROW himself, have known and described binucleate eggs. TROW in his last paper (p. 547) refers to the binucleate eggs of my form as of "occasional occurrence" and "in all probability of a pathological character." I stated expressly that they were "quite common" and I cannot see the slightest reason for suspecting them to be pathological. The cultures appeared perfectly healthy and the phenomenon was not infrequent as TROW implies. For these reasons I held that the number of nuclei in the ratio of 1:2:1, ordinarily accepted as evidence of fertilization when found successively in young and older stages of eggs and oospores, was insufficient for the establishment of sexuality in the Saprolegniales. To my mind proof is only furnished by clear and unmistakable instances of fusion between eggs and antheridial filaments and with the male nuclei actually *en route* to the female at the point

<sup>1</sup> TROW, A. H., On fertilization in the Saprolegnieae. Ann. Botany 18:541-569. pls. 34-36. 1904.

<sup>2</sup> DAVIS, B. M., BOT. GAZETTE 35: 233. 1903.

<sup>3</sup> TROW, A. H., Ann. Botany 13:131. 1899.

of fusion and within the egg. Few botanists would have been satisfied I think with Trow's evidence on the latter point in his paper of 1899. I regarded his views as "unproven and improbable" in the face of the mass of observations upon which most botanists have generally agreed that the Saprolegniales were apogamous. I still consider myself quite justified in taking this attitude, which I tried to present with due consideration to Trow as possibly being mistaken in his interpretation of some very difficult conditions. He seems to have taken my expressions as controversial, which I tried hard to guard against, and has certainly answered them in that spirit. One result at least has been an account of fertilization in *Achlya DeBaryana* which in detail of description and clearness of figures is quite a different sort of contribution from that of 1899.

*Achlya DeBaryana* furnished Trow the most complete series of stages of fertilization. In his *figs. 23-26* the antheridial filaments are united with the eggs by broad strands of protoplasm, and nuclei lie in some cases almost exactly at the points of fusion, either as though they had just entered the egg or were about to do so (*fig. 23*). The figures (especially *24* and *25*) even show that peculiar structure of the protoplasm which indicates a flow from the antheridial filaments into the eggs, conditions which have been illustrated many times in accounts of fertilization among the Peronosporales. These statements give us what we have a right to expect of any account of fertilization, and especially when the technical conditions are so complicated as in the Saprolegniales. They seem to me fundamental to the present problem, and the establishment of the ratio of nuclei in oosphere and oospore as 1:2:1 merely a corollary to the main proposition. If Trow will exhibit his preparation showing these protoplasmic fusions of antheridial filaments with eggs at scientific meetings in Great Britain or elsewhere he is not likely to have any difficulty in establishing his contention.

Of greater interest to me than the evidence of fertilization is Trow's account of a second mitosis in the oogonium and the origin of the aster-like structures which I discovered in Saprolegnia and considered coenocentra. During the second mitosis, according to Trow, two centrosomes with radiations appear at the poles of the spindle in anaphase, structures which were not present in the first mitosis. Some of these increase rapidly in size and become the centers of the egg origins, each one being accompanied by the nucleus that lay beside it, after anaphase of the second mitosis. Relatively few of the nuclei in the oogonium pass through this second mitosis, the remainder degenerating, and Trow believes that some of the daughter nuclei of this division with their asters also break down. The

surviving asters with their accompanying nuclei become the centers around which the cleavage of the protoplasm proceeds to form the eggs. Trow calls the egg-asters "ovicentra." He believes that the number of chromosomes shown in the first mitosis is reduced by half to form four in the second, so that the latter is a reduction division in oogenesis.

TROW'S account of the development of his ovicentra is fundamentally different from mine. I regarded them as simply representing dynamic centers of the protoplasm without any relation to mitotic phenomena, centrosomes, or asters, and as strictly comparable to the coenocentra of the Peronosporales. Trow considers them centrosomes in an aster (astrospheres) appearing at a final reduction division (second mitosis) in the oogonium. The situation has become very much complicated. If ovicentra are the same as coenocentra, why have not the latter been found associated with mitotic figures in the Peronosporales, where the structures are large and have been much studied? Is it possible that we have a new structure in the Saprolegniales? I am not willing to give up my view of oogenesis, although I can at once see the necessity of further investigation in both the Saprolegniales and Peronosporales. I do not think that Trow has presented enough evidence or treated the subject sufficiently with reference to the Peronosporales to be convincing. His theory is based, so I understand, chiefly upon the sections from one oogonium. There are some interesting questions suggested by the group of figures numbered 18, which one hesitates to ask without seeing Trow's preparations. But why are not the asters present at metaphase, the time when such structures are generally most conspicuous? And again, why are the asters sometimes so far away from the poles at anaphase (*fig. 18<sup>d</sup>*)? Is it possible that the "anaphase" is simply a resting nucleus drawn out towards a coenocentrum and attracted by it, as is the habit in the Peronosporales? These questions are not put in a captious spirit, but by one who is deeply interested in the problem and knows the difficulty of the investigations. Trow has advanced a most interesting hypothesis, which he must expect to be keenly scrutinized.

"The sperm nucleus soon after its entry into the oosphere acquires a distinct centrosome and astrosphere." This seems to the writer the most remarkable announcement in Trow's paper. Neither the origin nor the fate of this structure was followed. It looks exactly like an ovicentrum. The male and female nuclei and their accompanying astrospheres remain quite apart in the egg until the astrospheres disappear. In the meantime the oospore gradually fills with reserve material and the wall thickens. While these processes are under way the gamete nuclei fuse. The structure



of the egg when it contains two astrospheres with the gamete nuclei is of great interest, and this phase of the subject is worthy of extended study. I have seen and figured eggs in *Saprolegnia* with two coenocentra, each accompanied by a nucleus, when it was evident that the two were sister structures included within the same egg origin.

It is evident that very much more work must be done both in the Saprolegniales and Peronosporales before some of the points suggested by TROW's paper will be established. An ovicentrum arising from an aster associated with a reduction mitosis is a very different sort of conception from our present idea of the coenocentrum in the Peronosporales. The same sort of structure is also reported to appear suddenly beside the sperm nucleus after its entrance into the oogonium. It seems hardly conceivable that similar structures could behave in such different ways or could hold relationships to the coenocentra of the Peronosporales. Of course my own view of the essential agreement of the Saprolegniales and Peronosporales in processes of oogenesis around coenocentra must await the results of future investigations.—B. M. DAVIS, *The University of Chicago*.

#### THE SEXUAL ORGANS AND SPOROPHYTE GENERATION OF THE RHODOPHYCEAE.

OLTMANN'S theory that the structure developed from the fertilized carpogonium in the Rhodophyceae represents a sporophyte generation has received substantial confirmation in recent cell studies of WOLFE<sup>1</sup> on *Nemalion*. This investigation also makes an important contribution to our knowledge of the sexual organs of the red algae, establishing some complications of structure that are likely to prove very general in the group, and quite changes our conception of their morphology. Their possible relations to the sexual organs of the lichens, Laboulbeniaceae, and even to the Uredineae is full of interest.

The trichogyne of *Nemalion* contains a well defined nucleus which appears shortly after this structure begins to push upward from the carpogonium, but is only found in a fragmented condition in the mature trichogyne. The egg nucleus, which lies above the chromatophore in the carpogonium during the early development of the trichogyne, passes later to the bottom of the carpogonium. Although no mitotic figure was observed it seems clear that the nuclei of the trichogyne and egg are sisters, following a division in the terminal cell of the procarp.

These observations on *Nemalion* confirm my account of the trichogyne

<sup>1</sup> WOLFE, J. J., Cytological studies on *Nemalion*. *Ann. Botany* 18:607-630. pls. 40-41. 1904.

of *Batrachospermum*,<sup>2</sup> which I described as a nucleated cell with a chromatophore, and whose long life was accounted for by these complexities of structure. Later investigators, SCHMIDLE<sup>3</sup> and OSTERHOUT,<sup>4</sup> failed to find the trichogyne nucleus, but I am confident that my account of this structure is substantially correct. It is probable that nucleated trichogynes will be discovered in other red algae, and indeed they are likely to be quite general in the group, for the great length of these structures is much more readily understood as nucleated appendages than as cytoplasmic extensions from the small carpogonia. We shall have to recast our conception of the female sexual organ of the red algae. Instead of being a uninucleate cell (oocyst) with a filamentous cytoplasmic receptive outgrowth, we shall probably have at least a two-nucleate structure with the trichogyne obviously very much like a second cell in the organ.

These complications, puzzling at first thought, may clear up some very difficult problems of morphology. I refer to the multicellular trichogynes of the lichens and Laboulbeniaceae. They will not seem to be so far removed from the female organs of the red algae if trichogyne nuclei prove to be general, and we may come to regard them as the highest expressions of this growth tendency on the part of a primitive type of unicellular organ. BLACKMAN'S<sup>5</sup> recent investigations in the Uredinales indicate that female sexual organs are present in some forms (e. g., *Phragmidium*), and the presence of a sterile cell above the fertile is wonderfully suggestive of a trichogyne. All the female organs with multicellular trichogynes form a group quite by themselves, and apparently without relation to other multicellular sexual organs (gametangia). Since the cells are probably connected with one another by broad strands of cytoplasm, the physiological conditions may be very close to those of multinucleate sexual organs (coenogametes).

The sperm (spermatium) of *Nemalion* is formed singly in the spermatocyst and leaves this structure as a uninucleate naked or thin-walled mass of protoplasm. But before fertilization the original nucleus of the sperm divides with a mitotic figure, so that two male nuclei are formed and both enter the trichogyne. SCHMIDLE reported binucleate sperms in *Batrachospermum*, and some of my own figures show the same conditions, which, however, I explained as phenomena of fragmentation. It is evident that the sperm discharged from the spermatocyst (antheridium)

<sup>2</sup> DAVIS, B. M., *Ann. Botany* 10:49. 1896.

<sup>3</sup> SCHMIDLE, *Bot. Zeit.* 57:125. 1899.

<sup>4</sup> OSTERHOUT, *Flora* 87:109. 1900.

<sup>5</sup> BLACKMAN, *Ann. Botany* 18:323. 1904.

involves all of the protoplasm of this mother-cell, and the mitosis is a relic of times when more than one sperm was formed. The present binucleate sperm is a simple type of multinucleate gamete (coenogamete).

Both male nuclei are discharged into the trichogyne of *Nemalion*, which at the time of fertilization contains no organized nucleus. One male nucleus passes into the carpogonium, in the upper portion of which it meets the female nucleus and here fusion takes place. Several sperms may unite with and discharge their contents into the trichogyne, but supernumerary male nuclei soon break down. The fertilization of *Batrachospermum* undoubtedly takes place in essentially the same manner as described by SCHMIDLE and OSTERHOUT, but both of these observers failed to understand the complications of the trichogyne. On the other hand, I was misled by these complications and failed to discover the essential act of fertilization as a nuclear fusion in the carpogonium.

The development of the cluster of fertile filaments (gonimoblasts) follows the older accounts, but WOLFE contributes a new point of importance in showing that the carpospores are developed successively at the ends of the filaments. When one spore has been discharged the cell behind grows into the old cavity and develops there a new carpospore. This method of spore formation by successive proliferations is well known in certain groups of fungi, but among the algae has so far only been described for the Rhodophyceae.

The cytological evidence that the cystocarp is a sporophyte generation rests with a count of the chromosomes in mitotic figures at different periods of the life history. The number is about eight for the gametophyte, as shown in vegetative mitoses and during spermatogenesis. Mitotic figures were easily found at certain stages in the development of the fertile filaments (sporophytic), and these always presented an approximate double number of chromosomes, about sixteen. The numerical reduction of the chromosomes seems to take place just previous to spore-formation, for nuclear figures in the terminal cell of the older fertile filaments had quite the same appearance as those of the gametophyte and showed eight chromosomes. The manner of the reduction was not determined.

WOLFE gives some interesting details of cell and nuclear structure. The chromatophore of *Nemalion* has the form of a hollow ellipsoid, the center being a vacuole and not a pyrenoid. The chromatin of the resting nucleus is present in the form of a globular body (nucleolus). During prophase the chromatin passes along fibrillae to the nuclear wall. The spindle is intranuclear and centrosomes are present at its poles during metaphase.—B. M. DAVIS, *The University of Chicago*.

## CURRENT LITERATURE.

### BOOK REVIEWS.

#### The life history of *Pinus*.

DR. FERGUSON'S detailed account of this subject, profusely illustrated with excellent figures, will be useful as a reference work.<sup>1</sup> Much of the text and many of the figures have been taken from her previous papers, but the investigations have been pushed farther in every direction, so that the repetition adds to the value of the present account. The work deals primarily with *Pinus Strobus*, but conclusions are in most cases supported by observations upon several other species.

The titles of the five chapters are: microsporogenesis, the male gametophyte, macrosporogenesis, the female gametophyte, fertilization and related phenomena. In the appendix, several abnormal conditions are described.

In most species the archesporium is well developed before the approach of winter, but the mother-cell stage is not reached until the following April; in *P. Strobus* the archesporium does not appear until May. Probably there is a qualitative reduction of chromatin during the second mitosis in the pollen mother-cell. The air sacs arise by the separation of the exine from the intine at two definite points. A partial wall, lying within the intine at the prothallial end of the spore, is an interesting feature not hitherto described. The body cell ("generative cell") is not surrounded by a definite wall, and when its nucleus divides the two sperm nuclei lie free in a common mass of cytoplasm, never organizing distinct sperm cells. The two sperm nuclei are unequal in size and the larger one is always in advance.

The endosperm contains about two thousand free nuclei before walls begin to be formed. The archegonia appear about two weeks before fertilization. The independence of the male and female chromatin during fertilization, described by Miss FERGUSON and previous investigators, is here worked out in great detail. No cell walls are laid down at the base of the oosphere until the eight-nucleate stage of the proembryo has been reached. The divisions which result in the formation of four tiers of cells in the proembryo are described as taking place in the upper nuclei, which lie in the cytoplasm of the main body of the egg.

Miss FERGUSON'S conclusions are based upon an adequate field study and upon the examination of an immense number of preparations, so that the danger

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<sup>1</sup> FERGUSON, MARGARET C., Contributions to the life history of *Pinus*, with special reference to sporogenesis, the development of the gametophytes, and fertilization. Proc. Wash. Acad. Sci. 6:1-202. pls. 1-24. 1904.

of describing an occasional condition as a typical one has been reduced to a minimum.

It is due to Miss FERGUSON to announce that the manuscript left her hands Dec. 29, 1902, after which only a few minor corrections in the latter part of the work were possible.—C. J. CHAMBERLAIN.

#### MINOR NOTICES.

THE FIRST PART of the second supplement (1896-1900) of the Kew Index, containing the letters A-L, is ready for distribution. It is printed uniformly in all respects with the *Index Kewensis* itself. The advantage of having such a record of the years 1896-1900 cannot be overstated, and the tremendous amount of labor it involves on the part of Sir W. T. THISELTON-DYER and his colleagues deserves recognition from botanists. The American Branch of the Clarendon Press is at 91-93 Fifth Avenue, New York City; and the price of the part is 13s.—J. M. C.

KOORDERS and VALETON<sup>2</sup> have published another fascicle of additions to the known arboreal flora of Java. The five families included are Fagaceae (Castanea 3 spp., Quercus 25 spp.), Lauraceae (71 spp., 10 of which are new), Monimiaceae (4 spp.), Coniferales (Podocarpus 5 spp., one new), and Casuarinaceae (2 spp.).—J. M. C.

#### NOTES FOR STUDENTS.

INSECTS AND FLOWER COLORS.—Before considering some very recent papers on this subject, brief reference may be made to the work of PLATEAU, who more than any other investigator, has raised objections to the familiar "flag" or "signal" theory, as held by SPRENGEL, MUELLER, and DARWIN. Among the more striking of PLATEAU's observations,<sup>3</sup> we may note that he observed insect visits in normal number to heads of Dahlia, which were variously hidden from vision by means of leaves and papers; that the removal of the corolla from Lobelia flowers did not affect the insect visits, as claimed by DARWIN; that insects visit indifferently flowers of Salvia and Zinnia, similar in species but differing in color; that Pelargonium, however showy the flowers, is but little visited by insects normally, but that visits are readily induced in great numbers, if honey is placed on the flowers; that visits to Dahlia flowers cease if the nectar glands are removed, but begin again if honey is added; that the removal of the outer radiant flowers of Hydrangea has no effect on insect visits; that even such intelligent insects as bees commit many errors, visiting buds, wilted flowers, fruits, etc. In general

<sup>2</sup>KOORDERS, S. H., and VALETON, TH., Boomsorten op Java. Bijdrage no. 10. Mededeel. 'sLands Plant. no. 68. pp. vi+287. Batavia. 1904.

<sup>3</sup>See Bull. Roy. Acad. Belg., 1895, 1896, 1897; Mém. Soc. Zool. France, 1898, 1899, 1900; Ann. Soc. Entomol. Belg. 1901, 1902; Bull. Roy. Acad. Belg. 1902. Reviews of these articles in Biol. Cent. 16:417; 17:599; 18:469; 19:349; 20:490; 21:650; 23:224; 23:311.

it appears that PLATEAU's views have become less positive; he held at first that color and form have no influence in attracting insects to flowers. At present, while all color preference is denied, and while odor and the presence of nectar are believed to be the most potent attractive agents, he seems not to deny altogether the possibility of color attraction. PLATEAU's work has been accepted by but few students of flower ecology, and has been violently attacked especially by KIENITZ-GERLOFF.<sup>4</sup> PÉREZ,<sup>5</sup> while not calling PLATEAU's results in question, thinks that his conclusions are too one-sided. He holds that odor attracts at a distance, but that color serves to give directional precision close at hand. FOREL<sup>6</sup> thinks that PLATEAU and other authors have given insufficient attention to the memory sense of insects.

The immediate occasion for this review is the work of ANDREAE<sup>7</sup> and GILTAY.<sup>8</sup> ANDREAE begins his admirable treatise with the rather teleological statement that it is inconceivable that there should be so many showy flowers in the world, unless they are of some value to the plant, and that we cannot conceive of any use other than the attraction of insects! As the result of a great many ingenious experiments, he divides insects into two general groups: those with weak visual sense, short flight, and high odor sense; and those with opposite characters. The former group embraces lower forms for the most part, while the latter group, in particular, includes the Apidae and the higher Diptera. Thus, while many insects are attracted chiefly by odor, the bees and the higher flies are attracted chiefly by color. Bees tried to get inside of inverted glass vessels with flowers inside, while they paid little attention to open vessels with honey or perfume. A very gaudy artificial poppy had more visits than natural and less showy flowers, although it was observed that the insects soon learned to visit non-showy flowers containing honey and to avoid showy flowers that had no honey. Since the perception of odor is highly modified by direction of wind, moisture, and the presence of other odors, ANDREAE thinks that color is a much more reliable and effective attractive agent than odor.

The memory sense, touched upon by FOREL and ANDREAE, has been the special thesis for GILTAY's work, and his work seems to harmonize the discordant results of PLATEAU and ANDREAE. A new line of experimentation is suggested by his work on *Papaver Rhoeas*, a species whose flowers are self-sterile; from one group the petals were removed and the flowers left free for insect visitation, another group was left in the normal condition and free for insect visitation,

<sup>4</sup> See Bot. Zeit. 54:123; 55:84; 55:108; 56:138; Biol. Cent. 18:417; 23:557.

<sup>5</sup> See Act. Linn. Soc. Bordeaux, 1896; Mém. Soc. Sci. Phys. Nat. Bordeaux, 1903.

<sup>6</sup> See Zool. Jahresh. 1901.

<sup>7</sup> ANDREAE, E., Inwiefern werden Insekten durch Farbe und Duft der Blumen angezogen? Beihefte Bot. Cent. 15:427-470. 1903.

<sup>8</sup> GILTAY, F.: Ueber die Bedeutung der Krone bei den Blüten und über das Farbenunterscheidungsvermögen der Insekten. I. Jahrb. Wiss. Bot. 40:368-402. 1904.

while a third group had the corollas removed and was hand-pollinated. Instead of noting insect visits, the seeds from an equal number of flowers of the three groups were weighed. The average for each fruit was 117<sup>mg</sup> in normal insect-visited flowers, 115<sup>mg</sup> in the hand-pollinated flowers deprived of corollas, and but 50<sup>mg</sup> in the flowers deprived of corollas, which were left free for insect visitation. In other words a poppy with showy flowers produces more than twice as much seed as a poppy without showy flowers, when left free to insect visits. Thus GILTAY was at first led to doubt PLATEAU's conclusions. However, further experiments produced a modification of his views, since it was noted that insects, and particularly bees, pay less and less attention each day to showy flower groups where no nectar is present, while they pay more and more attention each day to inconspicuous flower groups, where nectar is present. It would seem, then, that PLATEAU failed to see the earlier visits of his insects, or at least failed to discriminate in his results between the earlier and later visits, while ANDREAE, in general, seems to have concluded his experiments too soon.—H. C. COWLES.

SCHMIDT<sup>9</sup> defines the mangrove association as that made up of tree-like evergreen plants which live near the strand of sea and estuary where the ground is constantly or at regular intervals flooded with salt or brackish water. Owing to its peculiar development and mode of life this is the most characteristic and well defined association known. The English "tidal forest" or the Holland "vlordborsch" is suggested as preferable to mangrove association, the former expressing exactly what is characteristic of the formation. The Barringtonia association (Schimper) borders closely upon the mangrove. As a rule, however, they are quite distinct, the Barringtonia being found on a higher level where the tidal water does not reach.

Light plays an important part in determining the position of the leaves and branches. By placing ten leaves horizontal and ten others upright in the normal light of the mangrove forest it was found that disorganization of the chlorophyll took place in one-half to two minutes in the former, while after thirty minutes only a partial disorganization occurred in the latter. By assuming the vertical position the buds and leaves expose the least surface to the direct rays of the sun. The relative intensity of the light according to the exposure of photographic paper is for the open sea one-fourth to one-half second, in the mangrove two seconds, and in the inland jungle ninety seconds. Hence it is seen that the light is very intense in the mangrove swamp. In the inland jungle the undergrowth does not arrange its leaves so as to get the least light, but so as to get the most, *i. e.*, in a horizontal position.

The major part of the article is devoted to taxonomic descriptions, emphasis being laid upon the arrangement and character of the buds, branches, and leaves.

<sup>9</sup> SCHMIDT, JOES., Bidrag til Kundskab om Skuddene hos den gamle Verdens Mangrovetraeer. (Contribution to the knowledge of the shoots of mangroves in the old world.) Bot. Tidsskrift 26:1-113. figs. 46. 1904.

No general uniformity exists in regard to the branching, although two general types may be separated: (1) the cymose, (2) the racemose. The leaves show considerable similarity in outline. Two type groups are made, the narrow leaved and the broad leaved type. The former type occurs only on species whose leaf-bearing branches are short and upright, while the broad leaves occur only on those whose branches are long.

In regard to protection of buds there is a considerable uniformity. *Rhizophora*, *Bruguiera*, *Ceriops*, *Kandelia*, and *Scyphiphora* are protected by means of axillary leaves which surround the developing parts; *Aegiceras* and *Xylocarpus* by means of true bud scales; *Lumnitzera* by red fleshy bud scales; *Avicennia* and *Sonneratia* by means of depressions in the leaf stalks. In comparison with northern trees, therefore, it will be seen that the majority of mangroves have buds similar to summer buds (*Platanus*), while *Aegiceras* and *Xylocarpus* correspond in this respect to the winter buds of northern latitudes.

The author criticises ARESCHOUG's work on the anatomy of mangrove leaves,<sup>10</sup> in that the latter author has not studied the plants in nature and his theory that salt-secreting hydathodes are general among mangroves is not proven in nature. That salt-secreting glands do occur is definitely proven, but only in the one genus *Aegiceras*.—G. H. JENSEN.

THE FINAL paper of BLACKMAN's studies on the fertilization, alternation of generations, and general cytology of the Uredineae has appeared,<sup>11</sup> presenting the subject more fully than the preliminary account which was reviewed in our April number.<sup>12</sup> We shall note at this time simply some additional details in this very clear and interesting paper.

The structure of the nuclei and processes of mitosis were studied, but it is evident that these subjects are very difficult. The chromatin remains for the most part in masses, so that chromosomes cannot be counted; but of course while there is but one mass throughout the gametophyte history from the teleutospore to the aecidium, there are two in the paired nuclei of the sporophyte. The nucleolus, always present, is extruded with each mitosis and formed anew in the daughter nuclei. A rudimentary spindle can sometimes be observed, with bodies at the poles which BLACKMAN calls centrosomes and which he believes arise by division, but his evidence seems insufficient on the latter point. The "conjugate" method of division of the paired nuclei only differs from that of single nuclei in the fact that two divide simultaneously side by side. The daughter nuclei remain entirely apart, so that the continuity of the chromatic material is not broken until the fusion in the teleutospore.

BLACKMAN points out the exact agreement of certain conditions in the Basidiomycetes with those in the Uredinales. Thus the mycelium preceding the basidium

<sup>10</sup> *Bibliotheca Botanica*, heft 56.

<sup>11</sup> BLACKMAN, V. H., On the fertilization, alternation of generations, and general cytology of the Uredineae. *Ann. Botany* 18:323-373. pls. 21-24. 1904

<sup>12</sup> *BOT. GAZ.* 37:320. 1904.



contains paired nuclei, which by fusion form a single nucleus in the mature basidium; the basidiospores are of course uninucleate, as is the mycelium that arises directly from them. Somewhere in the history of the mycelium the single nuclei must become paired. This will correspond exactly to the period of the aecidium in the life history of a rust, and must represent the time when an ancestral gametophyte developed sexual organs, now suppressed, and passed over to a sporophyte generation. The paired nuclei probably arise, as in the rust, by the union of neighboring cells in the mycelium, a process of apogamy, at the period when the sexuality is due.

It is important to note that the simpler types of life histories in the Uredinales where an aecidium is omitted must be regarded as derived from the *eu* and *opsis* forms by the entire suppression of cells which represent female sexual organs, and such life histories are in essential agreement with those of the Basidiomycetes which stand at the extreme in the process of reduction.—B. M. DAVIS.

JULES LAURENT<sup>13</sup> has given a detailed account of his experiments on the carbon nutrition of green plants. While the old humus theory was long ago abandoned, largely by reason of the work of LIEBIG, the tendency in recent years has been to hold to the utilization of organic foods to some extent, at least, by normal autotrophic plants. BÖHM, E. LAURENT, and ACTON have conducted rather conclusive experiments along this line, and a moderate amount of heterotrophic nutrition on the part of autotrophic plants is accepted by PFEFFER and JOST. The most conclusive experiments upon which this view may be based are those here considered, whose publication in full has been long awaited, since a preliminary notice was published in the *Comptes Rendus* for 1898. The chief reason for reposing confidence in LAURENT'S work is because he has worked with aseptic media, according to the most approved modern technique. Experiments with maize roots in contact with glucose solutions, in addition to DETMER'S solution, resulted in an increase of dry weight in the dark, whereas control cultures in DETMER'S solution only failed to show such increase in weight. MAZÉ has secured a like result with the vetch. Cultures in an atmosphere deprived of CO<sub>2</sub>, but exposed to light showed an increase of weight due to an intake of glucose by the roots. Various plant species, previously deprived of starch, whose roots were placed in 1 to 5 per cent. glucose solutions, the plants being placed under a bell-jar, over a potash solution and exposed to sunlight, showed the formation of starch from glucose that had been taken in by the roots. Similar results were not obtained in darkness, perhaps because less glucose was absorbed. Autophytes are found to differ from saprophytes not only quantitatively, as appears from the above, but also more fundamentally. Careful experimentation failed to disclose any power on the part of the roots of green plants to digest starch, a power possessed by holosaprophytes. A chapter is devoted to the consideration of the

<sup>13</sup> LAURENT, J.: Recherches sur la nutrition carbonée des plantes vertes à l'aide de matières organiques. *Rev. Gén. Bot.* 16:14-48; 66-80; 96-128; 155-166; 188-203; 231-242. 1904.

influence of organic substances on growth and form. In general, stem growth is checked in concentrated solutions. While this is doubtless partly due to the increased osmotic pressure, it is evident that chemical factors are also active, since glucose and glycerin solutions of equal concentration give different results. A final chapter deals with the application of his results to agriculture.—HENRY C. COWLES.

KIRKWOOD<sup>14</sup> has published the results of an extended investigation of Cucurbitaceae, chiefly relating to the development of the ovary and the embryo sac structures. The genera included are Fevillea, Melothria, Apodanthera, Bryonopsis, Trichosanthes, Momordica, Luffa, Cucumis, Lagenaria, Benincasa, Citrullus, Cucurbita, Sicyos, Micrampelis, Coccinia, and Cyclanthera, a remarkable list for one investigator in these days to present in a single paper; but the work has been under way since 1898. The mass of details will always be consulted for comparison with similar details in other families, and it is important to have so compact and clear a record. Certain general results, however, should be referred to even in a brief review. As is well known, the position of the family has always been a problem because of its contradictory characters, but it is generally placed now among the higher Sympetalae. It is interesting to note that Kirkwood has discovered that the sixteen genera studied unanimously contradict certain characters of Sympetalae that have been thought to be fundamental. The ovules of this great group is remarkably constant in its single and very prominent integument, its very much reduced nucellus, and its elimination of tapetal tissue (the hypodermal archesporial cell passing over directly into the mother-cell). In all the Cucurbitaceae studied, however, Kirkwood finds the ovules with two integuments, a well-developed nucellus, and tapetal tissue by no means eliminated, but often very extensive. It seems to the reviewer that just as the single character of polypetaly, arbitrarily applied, has detained the Umbelliferae among the Archichlamydeae, so the single character of sympetaly has forced the Cucurbitaceae among the Sympetalae. The synergids are remarkable for their prominence and structure, and the antipodals are ephemeral. Material did not permit a study of the peculiar pollen tubes reported for the family, or of fertilization and the development of the embryo. The endosperm is noteworthy for its extensive growth and nutritive activity, to which the author has given somewhat detailed attention. The general conclusions from the development of the ovary, especially the growth of the variable "placenta" and the origin of the ovules, are used in an interesting way to relate the genera in phylogenetic series.—J. M. C.

FITTING'S<sup>15</sup> preliminary report promises a paper which will be of special interest because he has attempted a solution of several of the most fundamental problems of geotropism. The behavior of orthotropic organs upon a klinostat

<sup>14</sup> KIRKWOOD, JOSEPH EDWARD, The comparative embryology of the Cucurbitaceae. Bull. N. Y. Bot. Garden. 3: 313-402. pls. 58-69. 1904.

<sup>15</sup> FITTING, H., Geotropische Untersuchungen. (Vor. Mit.) Ber. Deutsch. Bot. Gesells. 22: 361-370. 1904.

so arranged that the rotating plant describes a cone whose axis is inclined to the horizontal leads him to announce the following statements. The optimum position for geo-perception is horizontal and equal responses are induced by equal deviations above and below the horizontal. (In a recent paper NEWCOMBE<sup>16</sup> finds that roots and stems do not receive equal stimuli at equal angles above and below the horizontal.) The minimum perception time is extremely brief, less than two-thirds of a second. A proportionality between reaction time and perception time does not exist. Orthotropic organs can be geotropically stimulated even though the rotation be very rapid and uniform. There is a threshold-difference not only for intensity of stimulation but also for duration of stimulation, and for position during stimulation (deviation from horizontal). Intermittent is much less effective than continuous stimulation in the induction of geotropic curvatures. The response is little affected by the duration and number of individual stimulations. The presentation time is never smaller than for continuous stimulation, and is practically the same as for the latter when the ratio of stimulus duration to rest duration is as small as 1:5. The duration of single stimuli is without influence upon reaction time so long as the ratio of rest duration to stimulus duration does not exceed 5:1. Nothing was observed which would support HABERLANDT's statolith hypothesis.—RAYMOND H. POND.

SPINDLE FORMATION in the pollen mother-cells of *Cassia tomentosa* L. has been studied by HUS,<sup>17</sup> who finds that the cytoplasm of the young pollen mother-cell consists of a network of fibers more or less radially arranged, on and between which large and small granules are found. The meshes adjacent to the nuclear wall become smaller and elongated parallel to that wall. A granular zone appears around the nucleus; and at the same time there appears in the cytoplasm deeply staining rough fibers frequently arranged in conical groups. A felt-like zone, partially or sometimes completely surrounding the nucleus, next appears, and the deeply staining rough fibers of the cytoplasm, now united into cones, establish connection with the fibers of the felt-like zone. The linin threads become parallel with the other fibers and also parallel with the axis of the larger or ascendant cone. As soon as the rough threads of the fibers become smooth, the nucleolar wall breaks down, the linin and the kinoplasmic fibers anastomose and become grouped into bundles. A multipolar spindle is formed, two cones of which, opposite to each other, are more prominent and gradually absorb the smaller cones. The spindle of the second division is more pronouncedly multipolar than that of the first division. HUS concludes that "the spindle formation in *Cassia tomentosa* L. forms a connecting link between the multipolar polyarchal spindle *Anlage* ordinarily met with in dividing mother-cells of pollen, spore, and embryo-sac, and the multipolar diarchal spindle *Anlage* described for vegetative cells."—W. J. G. LAND.

<sup>16</sup> NEWCOMBE, F. C., Limitations of the klinostat as an instrument for scientific research. *Science* 20:376-379. 1904.

<sup>17</sup> HUS, HENRI T. A., Spindle formation in the pollen mother-cells of *Cassia tomentosa* L. *Proc. Calif. Acad. Sci.* III. 2:329-354. pls. 30-32. 1904.

LANG<sup>18</sup> has described in detail the single prothallus that he refers provisionally to *Psilotum*; otherwise the gametophyte of *Psilotaceae* is entirely unknown. During his expedition to the Malayan peninsula, LANG found a number of plants of *Psilotum* growing on the stems of tree ferns, with rhizomes embedded among the adventitious roots covering the stems. In close association with one of these plants the single prothallus referred to was found. A preliminary account of its external form was published in 1901. It is thick cylindrical, about 6<sup>mm</sup> long and 4.5<sup>mm</sup> in diameter at the broad upper end. It shows the usual differentiation of the subterranean gametophytes of *Lycopodium* into vegetative region below and sexual region above. The latter appears as a thick overhanging margin in which numerous antheridia occur. The sexual region does not contain chlorophyll, as in the *Lycopodium cernuum* type, the gametophyte evidently being entirely saprophytic. The vegetative region exhibits considerable histological differentiation, an endophytic fungus occupying a peripheral zone, and the central mass of tissue being entirely free from it. Some very interesting details in reference to the fungus are given, especially the occurrence of some remarkable multinucleate "vesicles" borne upon it. If this gametophyte is that of *Psilotum*, the genus is closely related to the homosporous *Lycopodiales*; if it is not, it is certainly the gametophyte of some *Lycopodium*.—J. M. C.

IN A RECENT number of *Science* MORGAN<sup>19</sup> attempts an analysis of the phenomena of organic "polarity." He opposes the "formative stuff" hypothesis of SACHS and others, or rather that feature of it which calls for the migration of specific formative material, and arrays considerable evidence against it. MORGAN'S conception is that while the material which gives rise to new parts is totipotent, it is not homogeneous, so that it is different at different levels of the body, this difference being graded from one end of the organism to the other. This accounts for the gradation in the facility with which new parts are formed from one end to the other. Morgan also recognizes an organizing principle, which he calls the property of "formative organization," "which acts on the new and old parts as a whole and determines the relative arrangement and proportions of the new organs."

In regard to "polarity" in plants Morgan maintains that these same principles hold. Assuming that there is a gradation from the distal to the proximal end of say, a mullen stem, in the size and vigor of the buds, the greater ability to produce shoots at the distal end is due merely to the fact that these buds are more vigorous and mature. The suggestion is made that the opposite may be true of the roots.—W. B. McCALLUM.

<sup>18</sup> LANG, WILLIAM H., On a prothallus provisionally referred to *Psilotum*. *Ann. Botany* 18:571-577. pl. 37. 1904.

<sup>19</sup> MORGAN, T. H., An analysis of the phenomena of organic "polarity." *Science* 20:712-748. 1904.

IN A COMMUNICATION to the Royal Society December 1, SCOTT<sup>20</sup> described a new type of strobilus belonging to the Sphenophyllales. The close affinity to Sphenophyllum is shown by the anatomy of the axis, which has the solid triarch wood characteristic of that genus, and by the fact that the whorled sporophylls are divided into dorsal and ventral lobes, as in all other known fructifications of this class. But, whereas, in all the forms hitherto described the lower or dorsal lobes are sterile, forming a system of protective bracts, while the ventral lobes alone bear the sporangia; in the new cone, dorsal and ventral lobes are alike fertile, and no sterile bracts are differentiated. Each lobe of the sporophyll divided palmately into several segments, the sporangiophores, each of which consisted of a slender pedicel, terminating in a large peltate lamina, on which two pendulous sporangia were borne. The wall of the sporangium has a rather complex structure, the most interesting feature in which is the well-defined small-celled stomium, marking the line of longitudinal dehiscence. The spores, so far as observed, are all of one kind; they are ellipsoidal in form, with longitudinal crests or ridges; their dimensions are 90-96  $\mu$  in length by 65-710  $\mu$  in width.—J. M. C.

THE COMMON *Ithyphallus impudicus*, generally considered to be a saprophyte only, has been found to be the cause of a destructive root rot of the vine in Hungary. According to the account given by ISTVÁNNFI<sup>21</sup> the subterranean part of the stem is entwined by a network of the characteristic cord-like strands of mycelium of this fungus. From these, branches are sent into the interior of the stem. Small roots are totally destroyed by strands which penetrate them lengthwise, destroying all the tissues and leaving only the thin decaying cortex. In the older roots the cortex and phloem are totally destroyed, leaving only a mass of debris. The wood cylinder is last attacked, but this also is finally destroyed, leaving only scattered remnants of the vessels. Destruction of the immature fruit-bodies and watering the exposed roots with fungicides is recommended as a means of prevention.

The same paper also contains an account of a mite, *Coepophagus echinopus*, which lives within and destroys the tissues of the roots of the vine. Not infrequently vines are attacked by both pests at the same time.—H. HASSELBRING.

SVEDELIUS<sup>22</sup> has published an account of *Enalus acoroides*, one of the marine Hydrocharitaceae growing on the coast of Ceylon; the subtitle being "A contribution to the ecology of the hydrophilous plants." The pollen grains are very large (about 170  $\mu$  in diameter) and heavier than sea water, owing to the presence

<sup>20</sup> SCOTT, D. H., On the structure and affinities of fossil plants from the Paleozoic rocks.—V. On a new type of sphenophyllaceous cone (*Sphenophyllum fertile*) from the Lower Coal-measures. Read December 1, 1904.

<sup>21</sup> ISTVÁNNFI, GY DE, Deux nouveaux ravageurs de la vigne en Hongrie (*Ithyphallus impudicus* et le *Coepophagus echinopus*). Ann. Inst. Cent. Ampélogique Roy. Hongrois 3:1-55. pls. 1-3. figs. 15. 1904.

<sup>22</sup> SVEDELIUS, N., On the life history of *Enalus acoroides*. Ann. Bot. Gard. Peradeniya 2:267-297. pl. 24. 1904.

of numerous starch grains. The wing-like leaves of the ovulate spathe aid in keeping the flower in a horizontal position, and the petals are specially adapted to catch the floating staminate flowers. The exposure of the ovulate flowers and the loosening of the staminate flowers occur only during low water. During high water the ovulate flowers are vertical; and the heavy pollen grains can scarcely avoid sinking down upon the erected stigmas. The pollination of *Enalus*, therefore, is both at the surface of the water and beneath it. The development of the embryo is of the ordinary *Alisma*-type, with a very large basal suspensor cell. At maturity the testa is an easily loosened cap around the embryo, the latter escaping entire and developing immediately.—J. M. C.

LOCK<sup>23</sup> has been investigating the rate of growth of the giant bamboo (*Dendrocalamus giganteus*) in Ceylon. The stems show a gradually increasing rate of growth up to 5<sup>m</sup>; then a nearly constant rate up to 15<sup>m</sup>; then a slowly diminishing rate to the final height of 30<sup>m</sup> or more. The average daily rate at a height of 1<sup>m</sup> is 10<sup>cm</sup> per day; at 5–15<sup>m</sup>, 30<sup>cm</sup>; and at 20–25<sup>m</sup>, 15<sup>cm</sup>. The greatest growth recorded in 24 hours was 46<sup>cm</sup>. The daily rate of growth is much increased by rainfall, the effect being greater the greater the height of the stem. The greatest change observed in rate of growth in two successive days was 50 per cent. of the average rate. Growth is almost always more rapid at night; the average hourly growth at heights of 3–12<sup>m</sup> between 7:00 A.M. and 5:00 P.M. being 6<sup>mm</sup>, and between 5:00 P.M. and 7:00 A.M. 16<sup>mm</sup>; the maximum rate being reached soon after dark. The curve of growth by day follows very closely that of the percentage moisture of the air.—J. M. C.

THE SECOND section of DAVIS'S<sup>24</sup> *Studies on the plant cell* is entitled, "Activities of the plant cell." The activities described are (1) vegetative activities, and (2) cell division. Cell division is treated under the subheads (a) the events of nuclear division and (b) the segmentation of the protoplasm. The account of mitosis in the thallophytes is particularly clear. The origin of the spindle is discussed in detail and considerable attention is paid to the centrosome problem. The view is expressed that all divisions of chromosomes are longitudinal. The evidence in favor of regarding the chromosome as a permanent organ of the cell is regarded as not yet sufficient. In dealing with the segmentation of the protoplasm, the author gives a valuable summary of recent work in this field.—CHARLES J. CHAMBERLAIN.

BURNS<sup>25</sup> concludes that in *Proserpinaca palustris* L. the water-environment is not the cause of the division of the leaf. He considers that the plant has two

<sup>23</sup> LOCK, R. H., On the growth of giant bamboos, with special reference to the relation conditions of moisture and the rate of growth. *Annals Bot. Gard. Peradeniya* 2:211–266. *pls.* 21–23. 1904.

<sup>24</sup> DAVIS, B. M., *Studies on the plant cell*. *Amer. Naturalist* 38:431–469. *figs.* 4–8. 1904.

<sup>25</sup> BURNS, G. P., Heterophylly in *Proserpinaca palustris* L. *Ann. Botany* 18: 579–605. *pl.* 38. 1904.

types of leaves, an adult and a juvenile type, the latter being the divided form. Under good vegetative conditions the former is produced, while under poor vegetative conditions the juvenile form is developed. A reversion from the adult to the juvenile form follows a change from a favorable to an unfavorable vegetative condition.—W. B. MCCALLUM.

LLOYD<sup>26</sup> calls attention to the parallelism between the results of his studies of the pollen tubes in the Rubiaceae and those of LONGO in the Cucurbitaceae. Each of these investigators has found that the pollen tubes vary greatly in behavior, even in closely related genera or species. They seem to have come independently to the same conclusion; that is, that endotropism and ectotropism are not distinct from one another; both regard the behavior of the pollen tube as a physiological character.—R. B. WYLIE.

WRIGHT<sup>27</sup> has published an extended account of the gross morphology, anatomy, and taxonomy of *Diospyros* as represented in Ceylon. The family is of such interest among dicotyledons that so extensive a study of living material is welcome. In the taxonomic portion of the paper twenty species are recognized and described in great detail.—J. M. C.

STUDENTS of plant-breeding will be interested in the results obtained by LOCK<sup>28</sup> in conducting a somewhat extensive series of experiments in Ceylon. In his first paper the details of the experiments indicate in the main a confirmation of MENDEL's law.—J. M. C.

<sup>26</sup> LLOYD, F. E., The pollen tube in the Cucurbitaceae and in the Rubiaceae. *Torreyia* 4:86-91. 1904.

<sup>27</sup> WRIGHT, HERBERT, The genus *Diospyros* in Ceylon: its morphology, anatomy, and taxonomy. *Annals Bot. Gard. Peradeniya* 2:1-106, 133-210. *pls.* 1-20. 1904.

<sup>28</sup> Lock, R. H., Studies in plant-breeding in the tropics. I. *Ann. Bot. Gard. Peradeniya* 2:299-356. 1904.

## NEWS.

PROFESSOR H. MARSHALL WARD has been elected president of the Cambridge Philosophical Society.

DR. J. F. GARBER (University of Chicago) has been appointed instructor in botany in the Yeatman High School of St. Louis.

MR. LUTHER BURBANK, so well known for his experiments in plant-breeding, has been appointed a special lecturer at Stanford University.

DR. J. C. ARTHUR has been appointed by the Botanical Society of America as its delegate to the International Botanical Congress at Vienna.

DR. MARIE C. STOPES (Munich) has been appointed assistant lecturer and demonstrator in botany in the University of Manchester, England.

WELLESLEY COLLEGE has received \$7200 from the ROBERT CHARLES BILLINGS fund, the income of which is to be applied to the needs of the department of botany.

WILLIAM R. MAXON, of the U. S. National Herbarium, left Washington December 12 for Guatemala, to be gone until May. Primarily he is to be engaged in cotton investigation.

PROFESSOR N. ONO, of the University of Tokyo, has been visiting the botanical laboratories of the United States on his way to the University of Leipzig for research in plant physiology.

C. R. BARNES, H. C. COWLES, and C. L. SHEAR were appointed delegates from the American Association for the Advancement of Science to the International Botanical Congress at Vienna.

MR. FRANCIS DARWIN who, upon his removal to London some months ago, retired from his position as Reader in Botany in Cambridge University, has been succeeded by Mr. F. F. BLACKMAN.

DR. R. S. WOODWARD, dean of the faculty of pure science in Columbia University, was elected president of the Carnegie Institution at the meeting of the trustees held at Washington, December 13.

THE ROYAL SOCIETY of London has awarded the Darwin medal of 1904 to Mr. William Bateson, "for his contributions to the theory of organic evolution by his researches on variation and heredity."

A CONTROLLING INTEREST in *The Plant World* has been purchased by Professor F. E. LLOYD, of the Teachers College, Columbia University, the journal passing under his editorial management at the beginning of the new year.



MR. R. P. GREGORY, demonstrator of botany at Cambridge University, has been awarded the Walsingham medal of the university for 1904, his thesis being "The reduction division in plants and its significance in the physiology of heredity."

THE Botanical Society of America elected as officers for the ensuing year: president, R. A. HARPER; vice-president, E. A. BURT; secretary, D. T. MACDOUGAL; treasurer, ARTHUR HOLLICK; councillors, L. M. UNDERWOOD, WM. TRELEASE.

DR. BURTON E. LIVINGSTON will sever his connection with the University of Chicago at the close of the winter quarter, having been appointed to the staff of the Bureau of Soils of the U. S. Department of Agriculture. He will take up his new duties at Washington on April 1.

PROFESSOR HENRY S. GRAVES, director of the Yale School of Forestry, has been commissioned by the Bureau of Forestry to do "inspection work" in the Philippines. During the winter his courses will be conducted by Professor B. E. FERNOW, formerly director of the Cornell School of Forestry.

BEGINNING with this year and volume 18, the *Beihefte zum Botanisches Centralblatt* which has attained an enviable reputation for the prompt publication of original papers of a high grade, will be issued under the same editors, Drs. UHLWORM and KOHL, by a new publisher, GEORGE THIEME, of Leipzig. Hereafter the journal will be published in two sections, the first to cover anatomy, histology, morphology, and physiology; the second being restricted to taxonomy, phytogeography, and like topics. The price of each section is to be M 16.

ALBERT GAUDRY, the eminent paleontologist, has headed a subscription for the erection of a monument to the memory of BERNARD RENAULT, whose untimely death this fall brought to a close those remarkable researches which have so greatly enriched the science of paleobotany during the past thirty-six years. It is proposed to erect this monument at Autun, France, RENAULT's native place and the scene of most of his labors. Subscriptions may be sent to M. BERTHIER, secrétaire de la Société d'histoire naturelle, 2 rue de l'Arbalète, Autun, France.

THE THREE botanical societies, Botanical Society of America, Society for Plant Morphology and Physiology, and American Mycological Society, through committees of conference, have agreed upon certain general principles, upon the basis of which they will fuse into one national society under the name, The Botanical Society of America. For some years the names of all the societies will appear upon official publications until the union becomes thoroughly known. There are to be two classes of membership, members and associates, the distinction being based upon published work. The fees are to be \$5 per year. Grants for research are to be made from the income. Meetings are to be annual, with no permanently organized sections, but free opportunity for local meetings or temporary sections in charge of committees. A joint committee has been formed to prepare a constitution for the united societies, which shall embody the principles agreed to, and to complete the reorganization, which is confidently expected to promote research and good fellowship among American botanists.

# BOTANICAL GAZETTE

FEBRUARY, 1905

## THE THEORY OF RESPIRATION.\*

CHARLES R. BARNES.

I ASK you to consider with me a topic which is of fundamental interest to physiologists, whether they concern themselves primarily with animals or with plants. I take it the basal identity of the living matter in all organisms and of its metabolism needs neither demonstration nor emphasis at my hands. Nor do I need to lay stress upon the importance of respiration as one of these metabolic phenomena, since it has been recognized from the earliest period as indispensable to life. The phlogiston theory of the composition of the atmosphere had scarcely disappeared below the scientific horizon, before the fact was discovered that there occur, in animals and in plants alike, an intake of oxygen and an output of carbon dioxide which are intimately related to their existence. This became obvious to man, of course, in his own experience, a very superficial study of the composition of the air inspired and expired from the lungs showing that it had lost oxygen and gained  $\text{CO}_2$ . This much of respiration was early recognized to occur also with the larger animals, and a few years later like observations were made upon plants by PRIESTLEY, and more accurately by LAVOISIER and INGENHOUS. Even this knowledge of respiration was not possible before PRIESTLEY's discovery of oxygen in 1774, and the very remarkable revolution in chemistry that followed in the closing years of the eighteenth century. Yet this disappearance of oxygen and formation of carbon dioxide are only the external indication of respiration, as has been long recognized.

\* Address of the retiring president before the Botanical Society of America, Philadelphia meeting, December 28, 1904. Published also in *Science*.

## RESPIRATION IN ANIMALS.

Upon undertaking special consideration of this topic, I found it needful to examine the recent literature of respiration in animals, the aspect of the general subject with which I felt myself least familiar. I found, to my very great surprise, that animal physiologists have concerned themselves very little with the essential problems of respiration. They seem to have been diverted to the study of the mechanism of gas movements in the higher animals. The lungs, with their intricate structure of lobes, lobules, atria, and air "cells;" the box in which the lungs are located, with its complex muscular mechanism, and the very complicated mechanism of innervation for the voluntary and involuntary movements which it executes; the blood, and the physico-chemical relation of the gases that enter and leave it in the lungs, of those that come into it from the tissues, and of those it gives up to the tissues—these are the topics that one finds exploited at length when he turns to the text-books. I diligently examined the most modern and most thorough text-books on animal physiology; such books as FOSTER'S *Physiology*; STEWART'S *Manual of Physiology*; the *American Text-book of Physiology*; and SCHAEFER'S *Text-book of Physiology*; but in them I found no treatment whatever, indeed no mention whatever, of the real problems of respiration, that is, of what is happening in the tissues—the processes of which these external phenomena are the sign. Yet this much-studied respiratory mechanism, which is so striking in the higher animals, is entirely wanting in the lower animals and in plants.

Not finding even a clue to the literature in the text-books, it was only after much search that I was able to discover that anything at all had been done; and it is *so* little that it is almost a negligible quantity. There is an obvious reason for this, beside mere interest in the more striking phenomena. I am intending, however, neither arraignment nor excuse, but a bare statement of what were to me rather surprising facts.

## RESPIRATION IN PLANTS.

The knowledge of respiration in plants began about the same time—the close of the eighteenth century—and advanced rapidly

on account of the notable revolution in chemistry which took place about this time. INGENHOUSS, the Dutch naturalist, really ascertained and published in 1779 the chief external facts of respiration; at least he was able to state them essentially as they were known for twenty-five years after his time. In 1804, DESAUSSURE showed that growth is dependent on respiration; that respiration is more active in growing parts than elsewhere; that it is the cause of the loss of weight to which plants are constantly subject; and later, that the heat set free in flowers is related to the absorption of oxygen. Not until 1833 was respiration treated comprehensively, when DUTROCHET expounded the subject, comparing the respiration of animal and plant, and showing it to be fundamentally alike in both.

Now at this point there began two remarkable misconceptions. One was the confusion that arose between respiration and the manufacture of carbohydrates, which DUTROCHET called "diurnal respiration." Of that I shall not speak, save to say that the great weight of LIEBIG's authority made this error persist for half a century.

#### RESPIRATION AND COMBUSTION.

The other misconception was engendered by the comparison of respiration to combustion. It had been observed by LAVOISIER that the heat of the animal body was dependent upon respiration; the heat of the plant body was shown by DESAUSSURE to be related to a disappearance of oxygen; combustion consumes oxygen and produces heat; therefore, respiration is a sort of combustion. So the argument ran.

It is quite impossible to overestimate the influence that this conception has had on the study of respiration. The mischief it has wrought depends chiefly, perhaps wholly, upon a misconception of the actual mechanism of combustion, a process that has ever been the *bête noire* of chemistry, as the history of the "phlogiston" theory well shows. To our changed conceptions of combustion I shall return later.

The idea of combustion, however, which dominated the argument I have cited, was that oxygen combined with carbon to form  $\text{CO}_2$  and with hydrogen to form  $\text{H}_2\text{O}$ . It was most natural, therefore, to conceive that the food taken up by the organism stood to it in

the same relation as does fuel to the engine, and that what happens is an actual oxidation of the food immediately and directly; in fact, a process precisely parallel to the burning of the same food outside the body.

One evident outcome of that idea is the current classification of foods into plastic and dynamogenous—those which are useful in building up the body, and those that are useful in producing heat within the body; into “fattening foods” and “heat-producing” foods. You are doubtless familiar with these phrases.

But if foods are “burned” in the body, it must be important to know how much oxygen enters it, and how much carbon dioxid and water leave it, so as to discern the ratio which exists between them. Plainly a basis for this must be a comparison of the differences between the combustion of foods outside the body and their “combustion” within the body. Yet, strangely, this has not been made until recently. Without giving the full tables, let me show the results arrived at by two observers, regarding two of the most common plant foods, glucose and tartaric acid. These observers assume, you will notice, that the processes are comparable. The results are stated as ratios of  $\frac{\text{CO}_2}{\text{O}_2}$ .

Food	By COM- BUSTION	By RESPIRATION	
		Diakonow	Purjewicz
Glucose - - - - -	$\frac{100}{100}$	$\frac{130}{100}$	$\frac{95}{100}$
Tartaric acid - - - -	$\frac{160}{100}$	$\frac{290}{100}$	$\frac{162}{100}$

DIAKONOW's whole series shows that in combustion the carbon dioxid was always less than in respiration; PURJEWICZ found (with the exception of tartaric acid, and even there the difference between his results and DIAKONOW's is in the same direction) that it was always greater, his results being absolutely different in significance from DIAKONOW's. And this is a good type of the results to be found in examining the literature! I am not now concerned in determining which set of results is correct, inasmuch as I believe

both are valueless, since on the assumption upon which they are based neither can be interpreted.

#### RESPIRATORY RATIO.

Long before this sort of comparison was made, however, a voluminous literature arose which was concerned only with the ratio between the carbon dioxid given off and the oxygen consumed, and how this ratio was influenced by temperature, by light, by this kind of food or that, by mere hunger, or by starvation. This ratio, the so-called respiratory ratio or respiratory quotient, the plant physiologists really inherited from the animal physiologists, by whom it was devised with reference to the gaseous exchange that occurs in the lungs. This respiratory ratio has proved a veritable will-o'-the-wisp, leading investigators into a bog where their labors and their thinking were alike futile. For as a sign of what is going on within, the respiratory quotient is absolutely valueless, however interesting the facts in themselves may be. I could cite an indefinite number of investigations to indicate this. I select a few cases.

As long ago as 1885, RUBNER showed<sup>1</sup> that the respiratory ratio varied in resting muscles at different temperatures.

At 8.4°	-	-	-	-	-	$\frac{\text{CO}_2}{\text{O}_2} = 3.28$
28.2	-	-	-	-	-	1.01
33.8	-	-	-	-	-	1.18
38.8	-	-	-	-	-	0.91

VON FREY and GRUBER<sup>2</sup> showed that in a dog's muscle, with artificial circulation, contractions are accompanied by an increase in the carbon dioxid added to the blood, but they found this increase variable (46-10 per cent.) and *less than the corresponding absorption of oxygen*, so that the respiratory ratio became lowered during contraction. TRISSOT<sup>3</sup> showed that the production of carbon dioxid in

<sup>1</sup> Versuche über den Einfluss der Temperatur auf die Respiration des ruhendes Muskels. DuBois-Reym. Archiv für Physiol. 1885:38-66.

<sup>2</sup> Versuche über den Stoffwechsel des Muskels. DuBois-Reym. Archiv für Physiol. 1885:533-562.

<sup>3</sup> Recherches sur la respiration musculaire. Arch. de Phys. Norm. et Path. V. 6:838-844. Also, Variation des échanges gazeux d'un muscle extrait du corps. Op. et ser. cit. 7:641-653. 1895.

excised muscles was increased if the muscles were killed by heat or were fatigued by prolonged stimulation. The output of carbon dioxid in such cases *was not related to the rate of absorption of oxygen*. Six years ago FLETCHER,<sup>4</sup> using Blackman's apparatus, the most intricate and accurate apparatus yet devised for following gaseous exchanges, showed that the evolution of carbon dioxid from excised frog's muscles is *independent of the amount of oxygen taken up during the period*. He distinguished in the production of carbon dioxid, first, a short period (about six hours), which he thinks dependent upon the presence of oxygen; and second, a long-continued evolution of carbon dioxid "due to chemical processes occurring spontaneously within the muscle, in which complex molecules are replaced by simpler ones, with the conspicuous results of the appearance of [sarcolactic] acid and of free carbon dioxid." He adds: "Under suitable conditions the occurrence of active contractions in an excised muscle is *not* accompanied by an increase in the rate at which carbon dioxid is yielded by the muscle," though oxygen is abundantly supplied then by the blood. He does find, however, an increased formation of other decomposition products.

CHAUVEAU and KAUFMANN, as long ago as 1887, found that the output of carbon dioxid from the levator muscle of a horse's upper lip was greater during activity than during rest, and *contained more oxygen than that absorbed in same time*.<sup>5</sup>

A great number of researches of the same tenor can be found in botanical literature. A single example must suffice. In an elaborate paper PURJEWICZ shows<sup>6</sup> that the variations in the carbon dioxid produced and the oxygen absorbed during a given period under various conditions *are not parallel*, the amount of carbon dioxid ranging within far wider limits than the oxygen. Thus, the carbon dioxid varied from —14 to 120 per cent. of the average; the oxygen varied from 0 to 48 per cent. of the average. PURJEWICZ, indeed, expresses his conviction that the respiratory ratio has no value as indicating the actual course of respiration, and would separate

<sup>4</sup> Survival respiration of muscle. Jour. Physiol. 23:10-99. 1898.

<sup>5</sup> Le coefficient de l'activité nutritive et respiratoire des muscles. Compt. Rend. Acad. Sci. France 104:1126-1132. 1887.

<sup>6</sup> Physiol. Unters. über Pflanzenatmung. Jahrb. Wiss. Bot. 35:573-610. 1900.

the taking up of oxygen and the production of carbon dioxide as two processes, only indirectly related.

It is clear that such results as have been cited became difficult to reconcile with the idea that respiration is combustion, and so an attempt was made to evade the force of the facts, while maintaining the comparison, by introducing a qualifying term and speaking of respiration as "physiological combustion." This modification, however, blinks the difficulty; it does not remove it.

Before passing from this part of my subject I may mention another false conception, which is more or less directly dependent on the notion that respiration is combustion. One often finds respiration described as a gaseous exchange—the taking up of oxygen and giving off of carbon dioxide—a trade between the atmosphere and the body. Clearly this is another case of transferring the superficial interpretation of our own physiological processes to other organisms. The exchange that takes place between the tissues and the blood, between the blood and air in the lungs, gives the foundation, and the unessential phenomena of respiration become substituted for the essential. It would be quite as correct to describe photosynthesis as "an exchange of gases," for carbon dioxide is taken up and oxygen is eliminated. Yet no one ever thinks so superficially of this process.

#### ANAEROBIC RESPIRATION.

For three quarters of the last century it was supposed that the evolution of carbon dioxide could only occur when free oxygen was available. But in the early seventies PFLÜGER discovered what seemed a peculiar form of respiration. He found that a frog put into a vacuum continued to give off carbon dioxide; and presently the same phenomenon was observed by PFEFFER and others in plants. So firmly had the conception of combustion fastened itself upon physiologists, that when this anaerobic respiration came to be explained, it was supposed that certain molecules of organic matter within the cell gave up their oxygen to others, that they might thus be burned in the body-furnace to yield energy. Hence arose the term "intramolecular respiration."

The study of anaerobic respiration, misleading as this early interpretation of it was, has thrown in late years a very great light



upon normal or aerobic respiration. Here is a process which results in the evolution of energy, and gives rise to one important end-product of aerobic respiration, viz., carbon dioxide; yet it early became evident that it could not be counted a process of combustion, at least in any sense in which combustion was then understood. Plainly, the changes that were going on within the organism, which enabled it to give off carbon dioxide when no free oxygen was to be had, could only be a rearrangement of atomic groups within the molecule and the formation of products which were simpler than those from which they arose.

#### FERMENTATION.

The process of fermentation, first thoroughly explored by PASTEUR, whose results have been much extended by the brilliant researches of HANSEN and many others, are evidently related to those of respiration by the nature of the end products and the conditions under which the processes occur. Indeed, when one compares the end products of respiration and of alcoholic fermentation he finds them to be identical in all respects. Other sorts of fermentation likewise yield many substances that are found originating in the metabolism of the higher plants.

We have, then, three modes of energy-release, which are evidently closely related, if not identical; aerobic respiration, anaerobic respiration, and fermentation. Their relations, so far as was known in 1898, were stated by PFEFFER in his *Pflanzenphysiologie* and need not be reviewed.

#### THE COURSE OF RESPIRATION.

In translating that work (p. 519) EWART wrote: "The actual course of respiration within the protoplast is quite obscure." PFEFFER himself says (p. 551): "Our knowledge of the inherent protoplasmic mechanism is too incomplete to afford a sound basis for any theory concerning the phenomena of respiration." Fortunately, knowledge in the last six years has broadened, and I believe that it is possible now to see pretty clearly what the actual course of respiration is. Perhaps you will say, to foresee rather than to see—but hypothesis must outrun demonstration. The advances to which we are indebted for deeper insight are in three fields: first, the chemistry of pro-

teids; second, the course of combustion, especially at low temperatures; third, the nature of anaerobic respiration, and its relation to aerobic respiration. Let me speak of these in order.

#### CHEMISTRY OF THE PROTEIDS.

A knowledge of the proteids, complex as they are, could be obtained only by a study of their decomposition products. Now there is a very remarkable uniformity in these decomposition products. No matter what the organism from which they are derived, no matter how simple they are or how complex, when broken up by the process of digestion, or by boiling with acids, they yield invariably a series of products which have become in the last few years much better known. These are amino- or amido-acids; such substances as leucin, tyrosin, arginin, glutamin, glycocoll, etc. Materials of this kind are invariably present, and certain ones are so invariably present that they can be used as the basis of distinctive tests for the occurrence of digestion or similar decompositions of proteids. This gave a clue to the nature of proteids which was followed by several observers, notably by KOSSEL, in the study of what are believed to be the very simplest proteids, because of the fewness and uniformity of the fractions into which they break up. These are the protamines. It has become clear from the study of these simple proteids that they are made up in somewhat the same way as the polysaccharides among the carbohydrates, that is by linking together a series of the amido-acids. This is possible because the amido-acids have a peculiar construction. They are, so to speak, different on different sides. On one side is an acid group and on the other a basic group; and so the amido-acids can hang together in chains, or even be condensed or polymerized to make a simple proteid. Among the amido-acids, as in the carbohydrates, there are certain atomic groups, like  $\text{CH}_3$ ,  $\text{CH}_2$ ,  $\text{CHOH}$ ,  $\text{CH}_2\text{OH}$ ,  $\text{COOH}$ , etc., which recur again and again, and in such groups the possibility of replacing a hydrogen atom or a hydroxyl radicle by some other atomic group is very great.

Note, for instance, the comparatively simple acetic acid,  $\text{CH}_3 \cdot \text{COOH}$ . If we replace one of the three H atoms by the amido group,  $\text{NH}_2$ , we have at once an amido-acid, glycocoll,  $\text{CH}_2(\text{NH}_2) \cdot \text{COOH}$ ,

which is one of the sorts of material out of which proteids can be made. Out of an alcohol or out of a sugar we get just the groups  $\text{CHOH}$ ,  $\text{CH}_2\text{OH}$ , etc., from which these amido-acids may be constructed when nitrogenous substances are present to supply the amido group  $\text{NH}_2$ . Thus the mode of construction of the proteids has been found to show a likeness to that of the complex carbohydrates, and it has long been known that the carbon groups were very much alike in both. It further appears that when the proteids are digested by any organism they break down into these fragments, of one sort and another, the amido-acids, the amides, etc., which may be put together again in new form to constitute the peculiar proteids of that particular organism. We may thus get one proteid out of any other by the breaking up of the complex molecule and the rearrangement of its constituent fragments. This fragmentation is readily accomplished by the proteolytic enzymes, which probably act on these bodies as the diastases do on carbohydrates.

#### OXIDATION.

The second important line of progress has been in the study of the oxidation of carbon compounds at low temperatures. For our purpose the important facts, which have only recently been developed, are that the oxygen of the air does not combine directly with carbon or with carbon monoxid to form  $\text{CO}_2$ , or with hydrogen to form  $\text{H}_2\text{O}$ , as has heretofore been supposed.

As long ago as 1893 DIXON's researches<sup>7</sup> on explosive gases showed that molecular oxygen was by far the most effective of the atmospheric gases in *retarding* combustion. This surprising result could not be interpreted then, and only in the light of TRAUBE's theory and the studies of BONE and others<sup>8</sup> on the oxidation of gases like methane and ethane at low temperatures, has it been possible to picture the mechanism of such combustion. This has been done by ARMSTRONG,<sup>9</sup> who holds (with TRAUBE) that the substances do

<sup>7</sup> The rate of explosion in gases. Phil. Trans. Roy. Soc. London A. 184:97-188. 1893.

<sup>8</sup> BONE and WHEELER: The slow oxidation of methane. Trans. Chem. Soc. London 81:535-545. 1902; 84:1074-1087. 1903.

BONE and STOCKINGS: Slow combustion of ethane. Trans. Chem. Soc. London 85:693-727. 1904.

<sup>9</sup> Retardation of combustion by oxygen. Chem. News 90:25. 1904. Mechanism of combustion. Trans. Chem. Soc. London 83:1088. 1903.

not undergo direct oxidation but hydroxylation, *i. e.*, its hydrogen atoms are successively replaced by hydroxyl radicles, with consequent splitting into various intermediate products, such as carbon monoxid and hydrogen peroxid, carbonic acid and water being the end products. ARMSTRONG says:

There is little reason to suppose that changes take place at high temperatures in rapid combustions in ways very different from those in which they occur at lower temperatures. . . . The effective operation is not the mere blow due to impact or the vibration caused by this in the molecule, but the conjunction of compatible molecules and the consequent formation of composite systems within which change can occur. In so far as temperature influences the formation of compatible systems, either as regards their character or the rate at which they arise, temperature has an influence, but probably not otherwise.

I ask you to notice, then, that the process of combustion is now being interpreted in the light of changes like those which have long been known in organisms under the name of hydrolysis, and are the characteristic mode of action of enzymes. Thus, when starch is acted upon by diastase it is probably by repeated reactions between water, dissociated into hydrogen and hydroxyl groups, and oxygen—in other words, by continued hydroxylation—that it becomes ready to fall apart into a series of dextrines and finally into maltose. Diastase in some way facilitates this dissociation. Maltase takes up the task, and maltose, further hydroxylized, cleaves into two molecules of glucose. Then zymase may lend its aid and hydrolyze the glucose molecule into lactic acid, breaking the latter still further into carbon dioxid and alcohol.

The mechanism of the digestion of starch is not known in detail, though the various intermediate products have been fairly well studied. The usual assumption made is merely that water combines with the starch under the action of diastase. I have carried the theory a little further into detail, as seems warranted by the studies of combustion. It is worthy of note also that the late steps in the process, the hydrolysis of glucose by zymase, have been designated by the term "fermentation." The combustion of starch has likewise not been examined, but as the end products are identical with those of digestion, it is not at all improbable that the intermediate steps are the same, though they succeed one another too fast to be followed by means at present available.

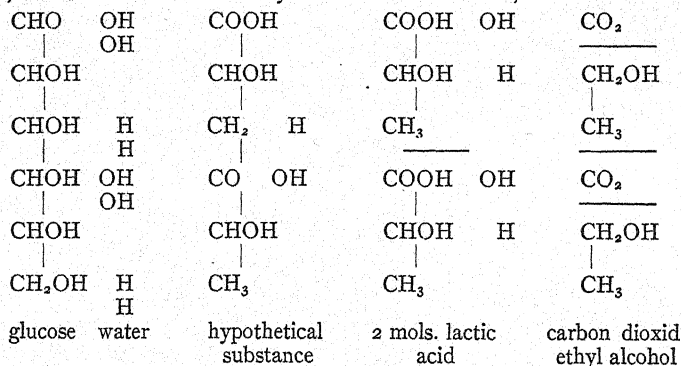
I need hardly remind you that our present ideas of the dynamics

of chemical reactions forbid us to believe that such dissociation does not go on slightly at low temperatures, even when unaided. But it is so slow as to be ordinarily beyond our measurement. The enzymes seem to be mere accelerators of the several processes, perhaps preparing "compatible systems," as high temperature may do in combustion; perhaps entering into union with the substance they act on and forming compounds which are dissociable at ordinary temperatures in appreciable amounts.

The clue to an understanding of respiration has been found, therefore, not by comparing it to combustion, which was so long misleading, but by assimilating combustion to respiration. We may hope that chemists will restrict the term "combustion" or introduce a new one that will make more obvious the mode of action. Physiologists at least will do well to drop "combustion" altogether from their vocabulary, as neither the past conception of it nor its probable use in the future conduces to clearness of thought.

#### NATURE OF ANAEROBIC RESPIRATION.

The third line of advance has been in a study of the relations of fermentation and anaerobic respiration. The first step was that long-sought discovery by BUCHNER, that the process of fermentation by yeast is brought about by the action of an enzyme which breaks up certain hexose sugars into carbon dioxid and alcohol. But a further step in advance has lately been taken. It appears from the work of BUCHNER and MEISENHEIMER<sup>10</sup> that the alcoholic fermentation is not direct, but that it occurs always in indirect fashion, as shown below:



<sup>10</sup> Die chemischen Vorgänge bei alkoholischen Gärung. Ber. Deutsch. Chem. Gesells. 37:419-428. 1904.

STĚPANĚK has reached the same conclusion,<sup>11</sup> and MAZĚ<sup>12</sup> has found acetic acid as an intermediate product in alcoholic fermentation by a different yeast. The interest of the discovery that inactive ethylidene lactic acid is the intermediate substance in this process of fermentation lies in the fact that one of the two acids of which that is composed namely, *d*-ethylidene lactic acid, or sarcosolactic acid, is formed as a product of respiration when proteids break down in the working, fatigued, or dying muscle. FLETCHER observed this as a more prominent product of contracting muscles than carbon dioxide itself. Thus a regular product of fermentation is also formed in the ordinary course of respiration.

The analogy between anaerobic respiration and fermentation had been suggested early—even by PASTEUR—and has thus been growing closer with each added bit of knowledge. But the precise way in which the destruction of the living substance went on in anaerobic respiration was still unknown. Fermentation had been shown to be due to an enzyme. Was anaerobic respiration also due to an enzyme?

Of course, enzymes are known to be present in a great many of the parts of plants, and the oxidizing enzymes seemed to be the sort to be sought. But none seemed to answer the conditions. At last, however, the object appears to have been attained. STOKLASA, in a series of papers published in various journals,<sup>13</sup> but all dealing with the same general problem, declares he has found in various tissues of animals, and in considerable number of plants, an enzyme analo-

<sup>11</sup> Ueber die aerobe und anaerobe Atmung der Eier. *Centralbl. Physiol.* **18**: 188–205. 1904.

<sup>12</sup> Utilization du carbone ternaire. *Ann. Inst. Pasteur* **18**: 277–303. 1904.

<sup>13</sup> STOKLASA: Identität anaerob. Atmung u. Gärung. *Oesterr. Chem. Zeit.* 1903. (Not seen.)

STOKLASA, JELINEK, and VITEK: Der anaer. Stoffwechsel der höh. Pfl. und seine Beziehung z. alcoh. Gärung. *Beitr. z. Chem. Physiol. u. Path.* **3**: 460. 1903.

STOKLASA and ČERNÝ: Isolierung des die anaer. Atmung der Zelle der höh. org. Pfl. und Tiere bewirk. Enzymes. *Ber. Deutsch. Chem. Gesells.* **36**: 622–634. 1903.

—: Ueber die anaer. Atm. der Tierorgane u. über die Isolierung eines gärungs-erregenden Enzymes aus dem Tierorganismus. *Zentralbl. Physiol.* **16**: 652–658. 1903.

STOKLASA: Ueber die Atmungsenzyme. *Ber. Deutsch. Bot. Gesells.* **22**: 358–361. 1904.

gous to BUCHNER's zymase, and like it-glycolytic. This enzyme he reports in leaves and roots of beet, tubers of potato, seeds, seedlings, and young plants of pea, seedlings of barley, and entire plants of *Paris quadrifolia*. Confirmatory results have (naturally enough) been obtained by several students or assistants who have evidently been engaged upon portions of the problem under the guidance of STOKLASA. It is only fair to say that MAZÉ has strongly criticised STOKLASA's methods from the bacteriological side, and declares himself unable to secure like fermentation under aseptic conditions;<sup>14</sup> though STOKLASA claims to have guarded carefully against infection and to have rejected contaminated cultures. Independently, MAZÉ has found what he calls zymase, in connection with pea seedlings, *Aspergillus* and *Eurotiopsis*. He declares it "an enzyme normal to all plants, arising like all other enzymes during vegetative (aerobic) life." In the higher plants, however, and in most fungi it "is oxidized with the greatest ease, so that one never finds more than a trace of it."

MAZÉ and STOKLASA interpret their results somewhat differently, MAZÉ holding the process of fermentation to be a nutritive one,<sup>15</sup> sugar being only assimilable when fermented and the nascent alcohol thus made available, while STOKLASA believes fermentation to be merely anaerobic respiration and essentially a process for the immediate release of energy.

Confirmation comes also from another source, for GODLEWSKI,<sup>16</sup> working with lupines, finds similar products, and concludes that their "anaerobic respiration is identical with alcoholic fermentation, of at least in essence dependent on it."

Moreover, KOSTYTSCHEW<sup>17</sup> and MAXIMOW<sup>18</sup> have found in *Aspergillus* an enzyme which is analogous to zymase and is responsible

<sup>14</sup> Various papers in *Annales Inst. Pasteur* 18: 1904.

<sup>15</sup> IWANOWSKY in 1894 propounded the theory that alcoholic fermentation is a pathological case in the nutrition of yeast, called forth by the abnormal composition of the nutritive medium.

<sup>16</sup> Weiterer Beitr. z. Kennt. der intramol. Atmung. *Bull. Acad. Sci. Cracovie* 1904:115-158. See also his earlier paper with POLZENIUSZ. *Bull. cit.* April 1901.

<sup>17</sup> Ueber Atmungsenzyme der Schimmelpilze. *Ber. Deutsch. Bot. Gesells.* 22: 207-215. 1904.

<sup>18</sup> Zur Frage über die Atmung. *Ber. Deutsch. Bot. Gesells.* 22:225-235. 1904.

for the formation of  $\text{CO}_2$  whether in aerobic or anaerobic respiration.

Thus several independent observers are testifying to the rather widespread occurrence of an enzyme which brings about a disruption of plant substance, under most varied external conditions, whether the plant be fed on one food or another,<sup>19</sup> this dissociation resulting in the formation of carbon dioxide and of various other products.

#### THE MECHANISM OF RESPIRATION.

Let us now focus the light coming from the chemistry of proteids, the mechanism of combustion, and the physiology of respiration, to form a picture of what goes on in the body.

*First:* We should conceive of the respiratory dissociation as taking place in the living material of the body and not in a food still unassimilated. Experiments with a wide range of foods have shown that they affect the intake of oxygen and the output of carbon dioxide in the most diverse ways, whence it has been assumed that the respiratory ratio varies because of the way in which the given food is oxidized. I do not say that it is not possible for the protoplasm to decompose a sugar directly or to oxidize a fat. But it must be remembered that in no case has it been experimentally proved that the food *is* directly attacked, and that all the facts can be explained on the other assumption, and some of them very much better than on the theory of direct oxidation. Moreover, the lability of proteids which have been raised to the life-level is their most striking characteristic as contrasted with their ordinary stability.

In such labile material the *second* step is easily conceivable. There occurs a shifting of the atomic groups within the molecule, perhaps as a result of the last step in their anabolism—the addition of hydroxyl groups from the water everywhere present. Dissociation follows necessarily; very slow perhaps at ordinary temperatures and with a scanty supply of water, yet sufficient evidently for the maintenance of life. Such conditions may very well be those obtaining in resting organs, spores, and seeds. But normally this cleavage may go on at a measurable rate, without anything more than the

<sup>19</sup> See a paper by KOSTYTSCHEW which has just come to hand (Ueber die normale und die anaerobe Atmung bei Abwesenheit von Zucker. Jahrb. Wiss. Bot. 40:563-592. 1904), showing the erroneousness of DIAKONOW's idea that anaerobic respiration is only possible when sugar is supplied.



inevitable dissociation when hydroxylation has progressed to a certain point. It seems, however, that there is generally—perhaps always—a hastening of this process, and that the highly unstable protoplasm is dissociated so rapidly that it liberates not only the energy immediately utilized in growth, movement, etc., but also an excess sufficient to be easily measured by so coarse an instrument as the thermometer. Catalytic agents like the enzymes are certainly (I think I may be permitted so strong an assertion) the usual accelerators. And it is highly probable that an enzyme identical with zymase or at least analogous to it, is an active though secondary agent in this acceleration. It may very well be also that those changes outside the protoplast (whether without the organism or not) that are called stimuli accelerate still further the katabolism, even to an explosive speed in some cases.

This primary dissociation may plainly be independent of free oxygen, though it is hardly conceivable that there will not be some oxygen present unless the plant has grown under most unusual conditions, which one can scarcely realize experimentally. The products of this decomposition are not sufficiently known, nor is their precise character important for our discussion. Among them are certainly the more complex amido-acids, carbon dioxide, and alcohol.

*Third:* Up to this point the respiratory processes are quite alike whether the plants grow in the air or apart from it. If sufficient oxygen be not present, the disruptive processes may reach an equilibrium, just as an electrolyte practically ceases to pass a current of electricity unless a depolarizer be present. So in the hydroxylation of proteids, there is needed some substance to disturb constantly, in one direction or another, the equilibrium that tends to be reached. The common agent in this is oxygen. Of course, oxygen can hardly be the only depolarizer that can promote further action. Thus, MAZÉ found the presence of levulose conduced to the continued evolution of carbon dioxide in the absence of oxygen, and it is quite possible that levulose took up the rôle of depolarizer, though MAZÉ does not so interpret his observation.

In anaerobic respiration insufficient oxygen is supplied. Its products that have been most observed, and are therefore (though doubtless groundlessly) counted its characteristic products, are carbon

dioxid and alcohol. Indeed, lactic seems an equally characteristic though transient product. The fact that hydrogen has also been often recognized among them supports the interpretation of the function of oxygen just suggested, and accords thoroughly with the theory of hydroxylation. In that process hydrogen atoms from the dissociation of water would be left free in case there was insufficient oxygen to form  $H_2O_2$ .

*Fourth:* But if the organism can get an adequate supply of oxygen, the katabolism continues, some of the most complex previous products breaking up by hydroxylation and thermal cleavage. Among the fragments are undoubtedly some that lose in part those very groups in which sugars, alcohols, fatty acids, etc., are peculiarly rich. These are rebuilt at the expense of such foods, which therefore disappear as a result of respiration. That ethyl alcohol does not persist when oxygen is present may mean either that it is decomposed, or that in its nascent state it is assimilated in the rebuilding of proteids, for we have seen how easily acetic acid, one of its oxidation products, can be converted into an amido-acid, glycocoll, and be thus in direct line for reconstructive metabolism.

This, in its fundamental features, is the theory I have presented in lectures to advanced classes since 1898, though always as more or less a speculation. For various details I am indebted to the recent literature, already cited. Because it is capable of explaining the observed facts, which are now sufficiently numerous to demand a coherent explanation, I conceive it to be entitled to the dignity of a theory. Time forbids the discussion of details, and many points have been considered that cannot be here presented.

This theory maintains the direct relation of aerobic and anaerobic respiration, whose genetic connection was long since advocated by PFEFFER. Anaerobic respiration is the primary process in all organisms. Whether aerobic respiration occurs or not depends upon the availability of oxygen. The relation of fermentation to the process is not wholly clear; for although fermentation gives rise to the same products as anaerobic respiration, this may depend in part upon respiratory decompositions, such as have been described, and in part upon digestion, which, as IWANOWSKY and MAZÉ think, render the alcohol from sugars available for assimilation. I am inclined to

believe that in fermentation we deal with an exaggerated anaerobic respiration, the active ferments being plants in which zymase is produced in such amounts that it can attack sugars outside the organism, and thus secure sufficient energy with a minimum destruction of the protoplasm.

#### ENERGESIS.

Finally, I may suggest that for didactic purposes it is desirable to have a word other than "respiration" to designate the disruptive processes by which energy is released, leaving "respiration" to designate the more superficial phenomena of aeration with which plant physiologists are but little concerned. Perhaps the word "respiration" is already too firmly imbedded in literature to be so limited. It will at least do no harm to propose that the terms "aerobic and anaerobic *energesis*" be considered, to which "fermentative *energesis*" may be added if necessary.

THE UNIVERSITY OF CHICAGO.

THE FORESTS OF THE FLATHEAD VALLEY, MONTANA.<sup>1</sup>  
CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY.  
LXVII.

HARRY N. WHITFORD.

(WITH MAP AND TWENTY-THREE FIGURES)

INTRODUCTION.

THE factors concerned in the grouping of plants are classified by SCHIMPER<sup>2</sup> as climatic and edaphic. When the climate of any region is such that a particular form of plant is favored, in most instances it gives character to the vegetation. For example, in the eastern United States the climate favors the tree form and gives rise to a "forest formation." If the grass form predominates, however, a "prairie formation" is the result. Again, if the climate be such that the cactus form gives the tone to the landscape, the "desert formation" is developed. Two such formations are shown in *fig. 1*, which is a view of a portion of the Flathead valley looking west from a high mountain. In the distance on the west side of the valley is a prairie formation; on the east side is a forest formation.

However, if one stands on a mountain top and looks down into these formations, he will observe that isolated areas in the forest do not contain trees, but may have a prairie, a swamp, a clearing, or a heath. The prairie formation may contain forests along streams or on protected hillsides. Also, in the forest formation there may be areas occupied almost exclusively by one, two, or more species of trees; while at a little distance there may be another area with entirely different trees. In other words, the composition of the forest changes from place to place. To distinguish these local groups from the general climatic grouping, SCHIMPER has called them "edaphic formations." By other authors they have been called "plant societies," "plant associations," or merely "plant forma-

<sup>1</sup>This paper is based on work as a collaborator in the U. S. Bureau of Forestry, to which acknowledgment is here made for permission to publish.

<sup>2</sup>SCHIMPER, A. F. W., *Plant geography upon a physiological basis* (translated by FISHER) 159-161. 1903.

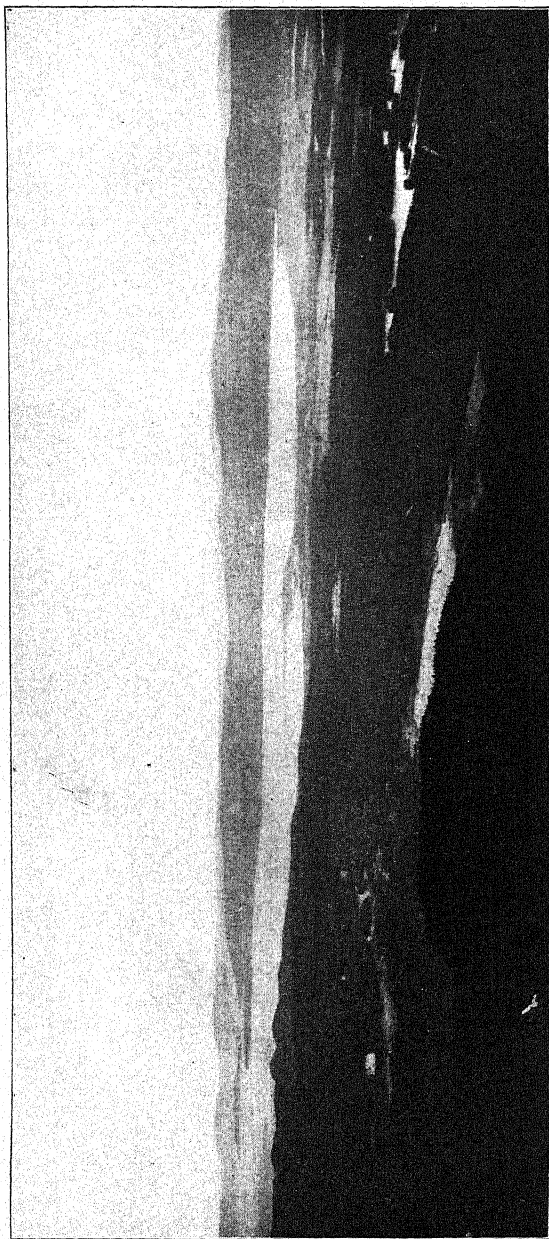


FIG. 1.—View looking southwest from a high point in the Swan Mountains from just beyond the northeast limits of the map; Flathead Lake in the distance; the point of land extending into the lake is the delta of Flathead River; on the west side of the valley at the head of Flathead Lake a prairie formation; on the east in the foreground a forest formation. The edaphic areas shown in the forest formation are Ross Lake in the immediate foreground; north and south of this meadows; to the right Echo Lake; midway between Ross Lake and the delta is "nigger" prairie. In the prairie formation the course of Flathead River may be seen by the line of forests along its banks.—From photograph by ELKROD.

tions.”<sup>3</sup> *Fig. 1* will also illustrate these smaller groups. In the foreground may be seen a pond which contains its characteristic plants; to the right of this a meadow; and between the pond and Flathead Lake a local prairie. These are in the forest formation. While the soil factors determine primarily the variety of the plant landscape, other factors must be taken into consideration. In this paper, however, the convenient term “edaphic formation” will be used.

COWLES<sup>4</sup> was the first to show clearly that plant societies are not static, but dynamic. In brief, his contention is that the plant society changes with the physiographic changes that are constantly going on. In a former paper<sup>5</sup> I have attempted to correlate the various plant societies found in northern Michigan. In that study it is shown that the region lies in a deciduous forest formation, and that while the coniferous forest societies are present in the more xerophytic conditions, there is a tendency for them to be replaced by the climax society, the beech-maple combination. The present study, made in a region with a somewhat different climate, was undertaken to determine whether the various plant societies could be correlated in the same way. For this purpose a general survey was made of the Flathead valley, and a portion of it was selected to study in closer detail. No attempt was made to study the conditions in the higher altitudes where a different climate prevails.

#### PHYSIOGRAPHY.<sup>6</sup>

There exists a close relation between the development of the physiography of a region and the life history of its forest formation; hence the necessity of describing the topographic features of the Flathead valley. It is a well-defined physiographic unit, situated in the northwestern part of Montana, about long. 114° 30' W. and lat. 47° 30'–49° N. (*fig. 2*). The altitude of the valley is approxi-

<sup>3</sup> For a discussion of the subject, see COWLES, H. C., The physiographic ecology of Chicago and vicinity. *BOT. GAZETTE* 31:74–76. 1901.

<sup>4</sup> *Loc. cit.* pp. 75–108, 145–182.

<sup>5</sup> WHITFORD, H. N., The genetic development of the forests of northern Michigan. *BOT. GAZETTE* 31:289–325. 1901.

<sup>6</sup> See ELROD, M. J., The physiography of the Flathead Lake region. University of Montana Bull. 17: 197–203.

mately 900<sup>m</sup>, and it extends from the Canadian boundary about 160<sup>km</sup>, a little to the east of south, to the low Jocko Mountains. A number of mountain ranges form its western border, and the front range of the Rocky Mountains with sub-ranges lie directly east, the

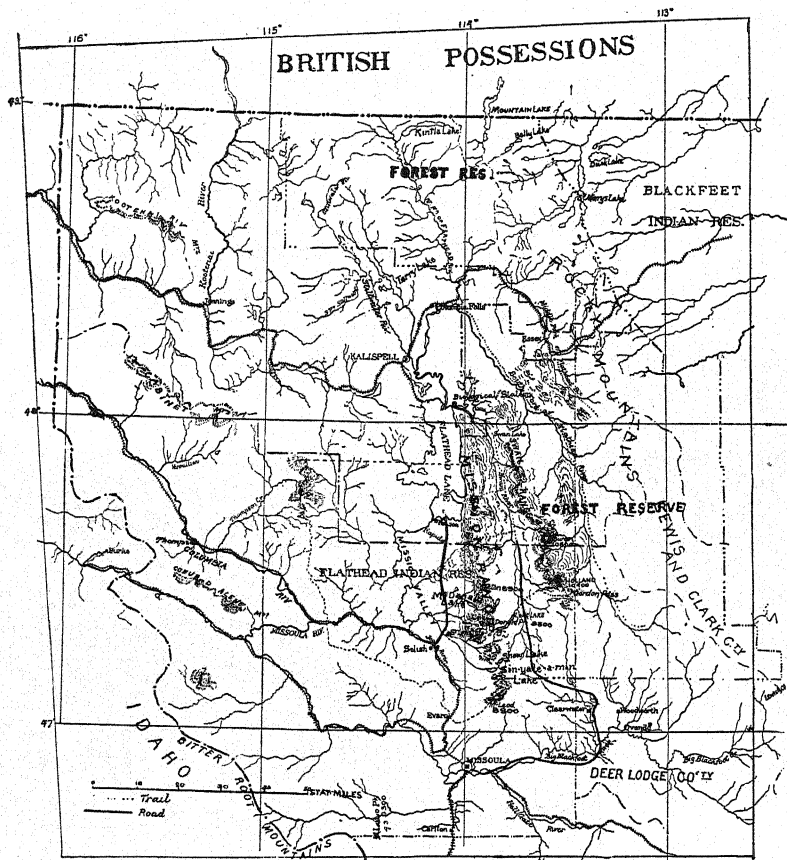
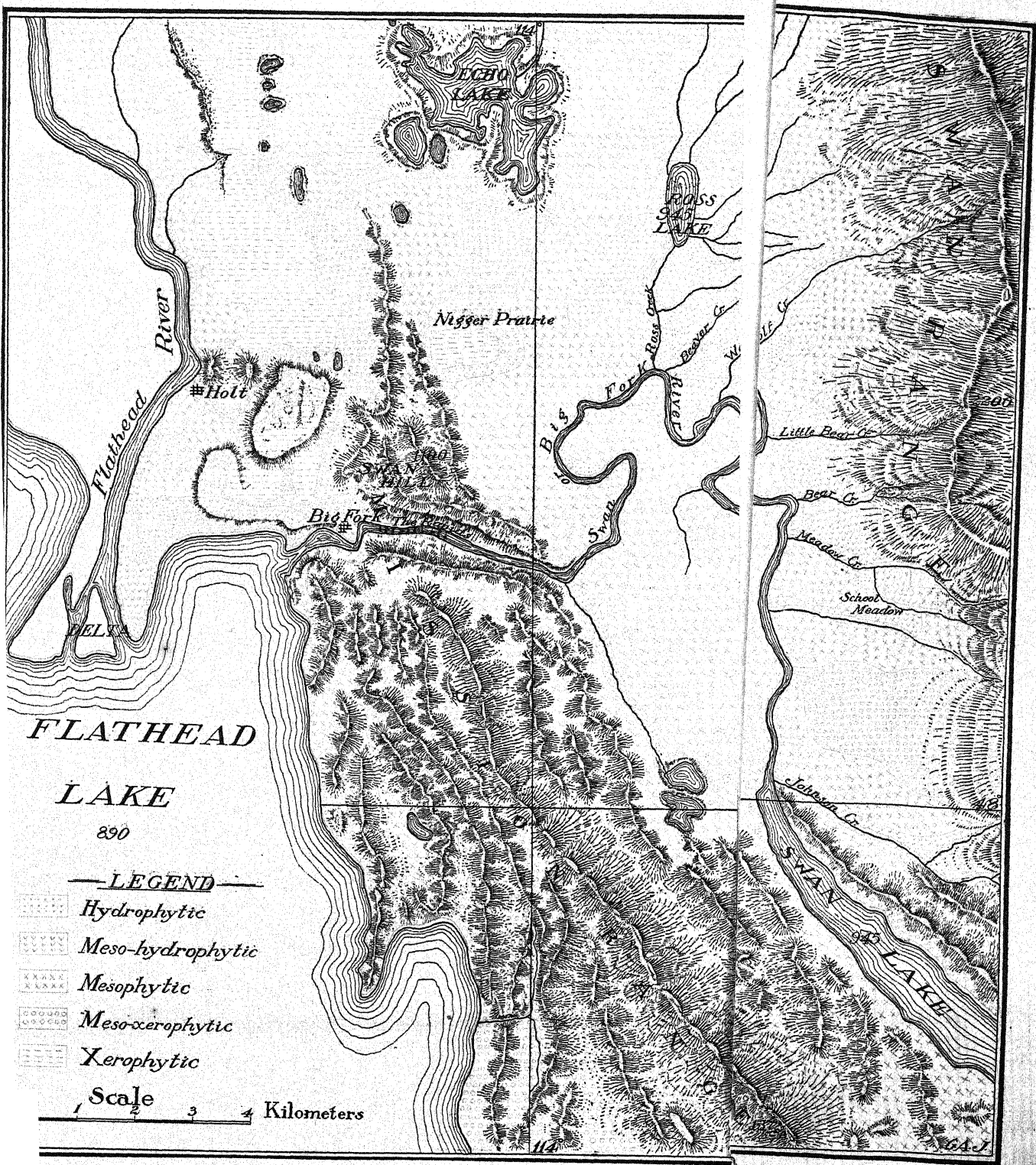


FIG. 2.—Map of northwestern portion of Montana, showing the general location of Flathead valley.—After ELROD.

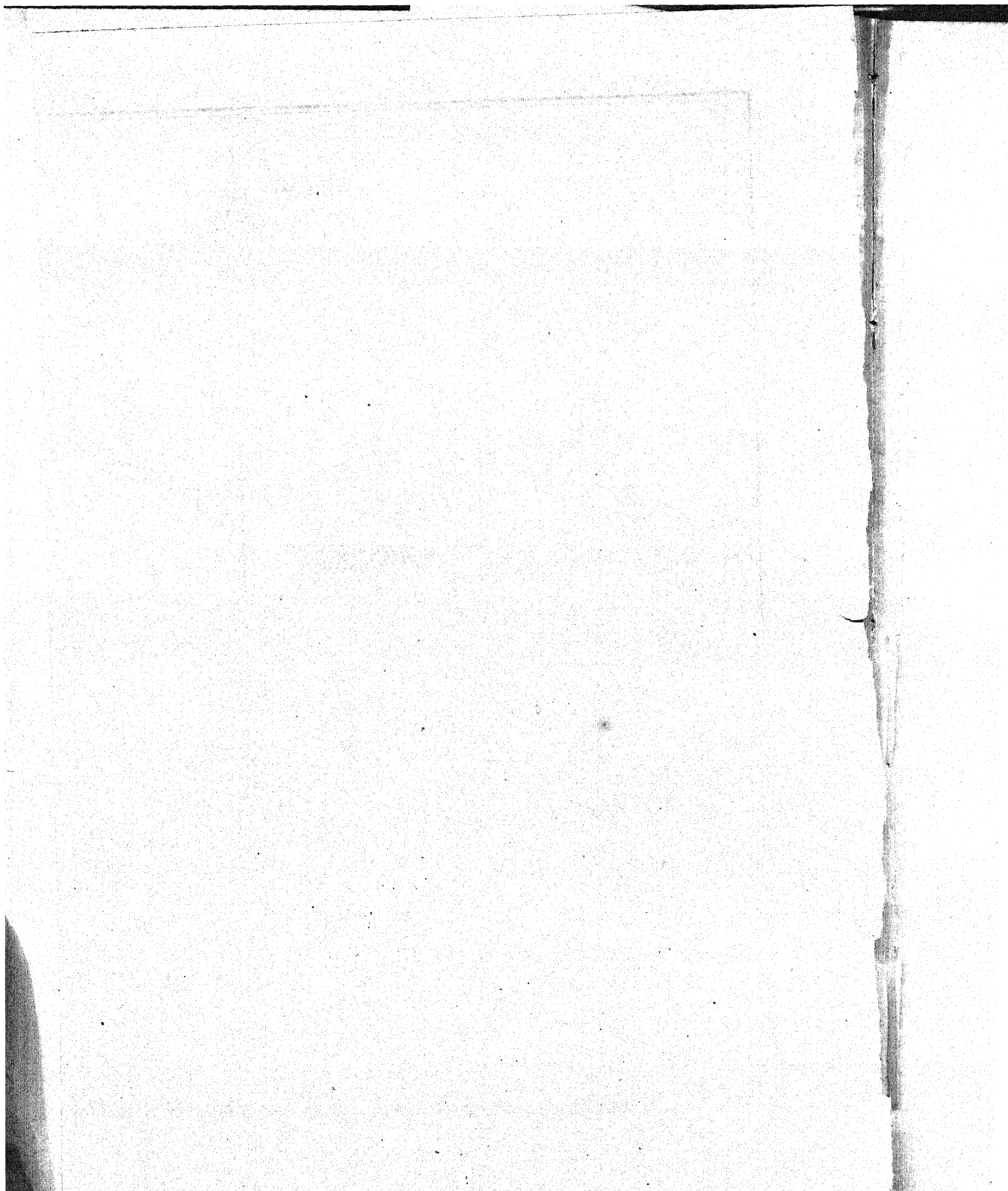
valley varying in width from 16 to 40<sup>km</sup>. The portion lying south of Flathead Lake is known as the Mission valley. That part with which this paper deals more especially is found in the region bordering the northeastern shores of Flathead Lake (*fig. 3 and map*).

The main drainage system of the valley consists of the Flathead











Lake; its principal inlet, Flathead River; and its outlet, the Pend d'Oreille River. Flathead River is formed by the confluence of three branches known as the North Fork, South Fork, and Middle Fork, all of which rise in the Rocky Mountains. These flow for their entire course in valleys in the mountains and unite to form the main river near Columbia Falls. The Stillwater and Whitefish Rivers are the principal branches that lie in the Flathead valley. For about the lower half of its course through the valley, the Flathead River is a broad, sluggish, navigable stream that is constantly depositing sediment. Especially is this the case at its mouth, where a delta about 3<sup>km</sup> in length has been formed (*fig. 4*).

Flathead Lake (*fig. 5*) is some 40<sup>km</sup> from north to south and varies in width from 10 to 20<sup>km</sup>, its altitude being 890<sup>m</sup>. It is a remnant of a former lake of much greater extent, which probably covered a large portion of the valley at its head. An old outlet near Dayton (*fig. 3*), some 120<sup>m</sup> above the present level of the lake, and terraces at approximately the same height, indicate the former distribution of the waters of the lake. The Pend d'Oreille River (*figs. 5, 6*), the present outlet, has cut its way through a huge moraine at the foot of the lake. This moraine no doubt acted as the dam that backed up the water over the low valley lying to the north. The river rapidly cut its way through this moraine until its present condition was developed. This erosive process is going on much more slowly today because the river channel has reached bed rock.

The Mission Range lies to the east of the lake and the Mission valley. This is a distinct range separated from the other mountains on the east by the Swan River valley. It has an altitude of approximately 2750<sup>m</sup> at its southern end. From this altitude the mountains become gradually lower until near the north end of the lake, where they merge imperceptibly into the valley. The Swan River valley opens into the Flathead valley where these mountains end (*map* and *fig. 1*). It is in reality only an arm of the latter, and during the time of the greatest extension of Flathead Lake the water probably backed up into this valley and formed an embayment. As the Pend d'Oreille River cut its way through the moraine at the foot of Flathead Lake, the level of the water in this embayment was lowered. But some time before the present condition was reached, a moraine

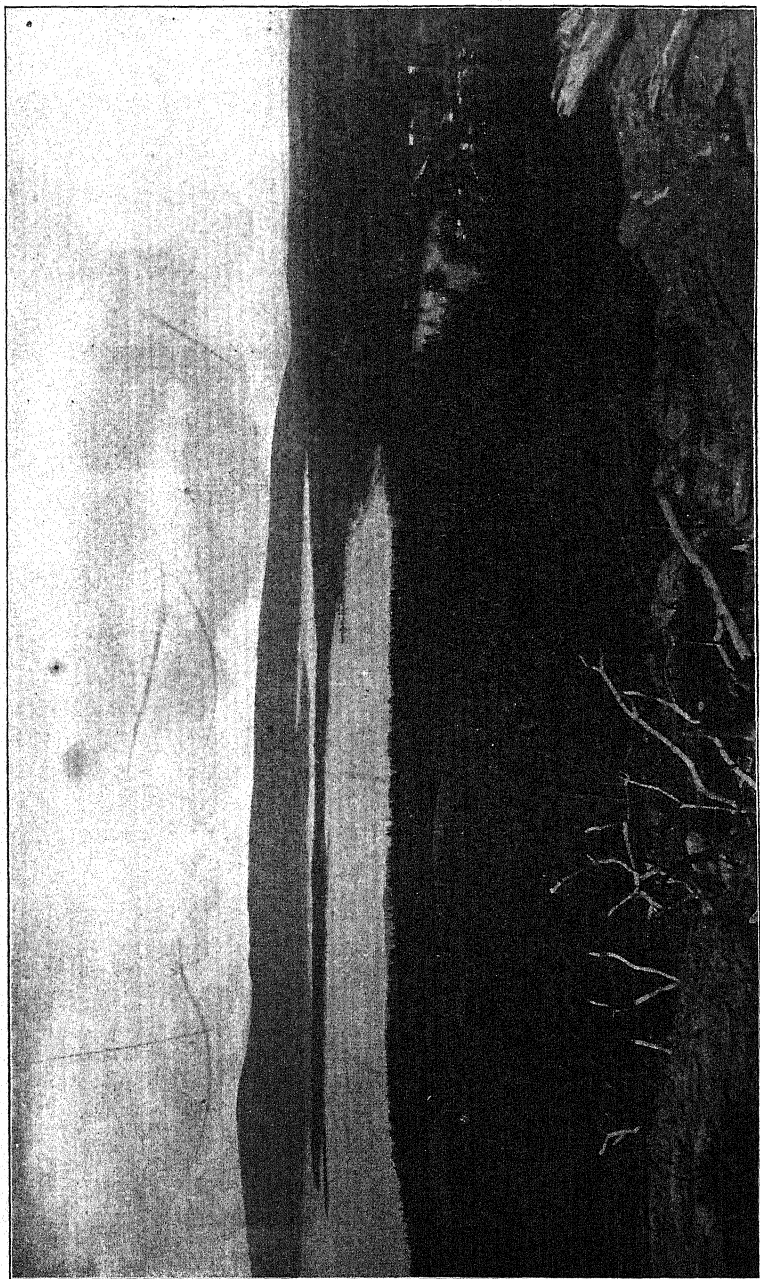


FIG. 4.—Looking west from Mission Mountains across the northern end of Flathead Lake; the delta is seen in the distance; on the right is the town of Big Fork near the mouth of Swan River; beyond Big Fork is a portion of the prairie region; in the center and on the left is the forested region on the west slopes of the Mission Mountains; the forests here have been nearly destroyed by fire.—From photograph by ELROD.

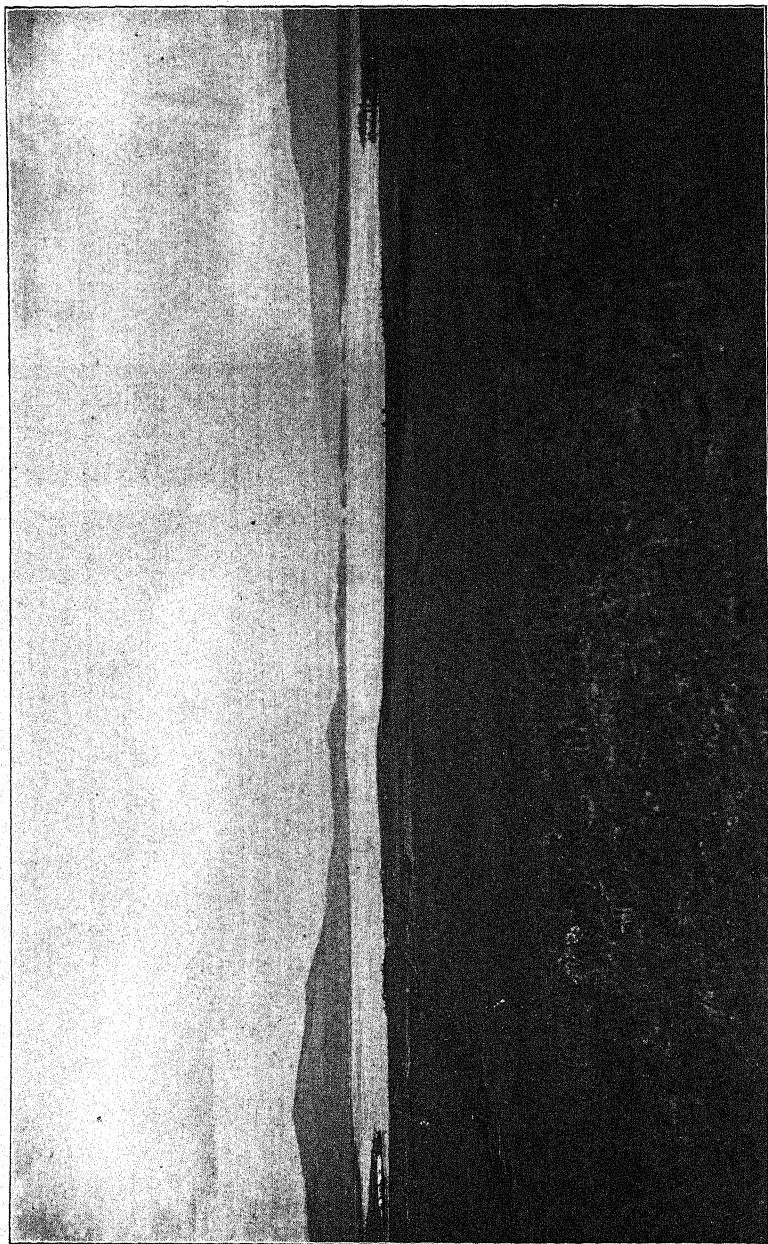


FIG. 5.—Flathead Lake looking north from moraine at south end; in the distance a chain of islands stretching nearly across and dividing the lake into two unequal parts, the greater portion being to the north; the islands mark the beginning of the forested region; to the left the outlet of Pend d'Oreille River, a part of which is seen in *fig. 6*.—From photograph by ELKON.



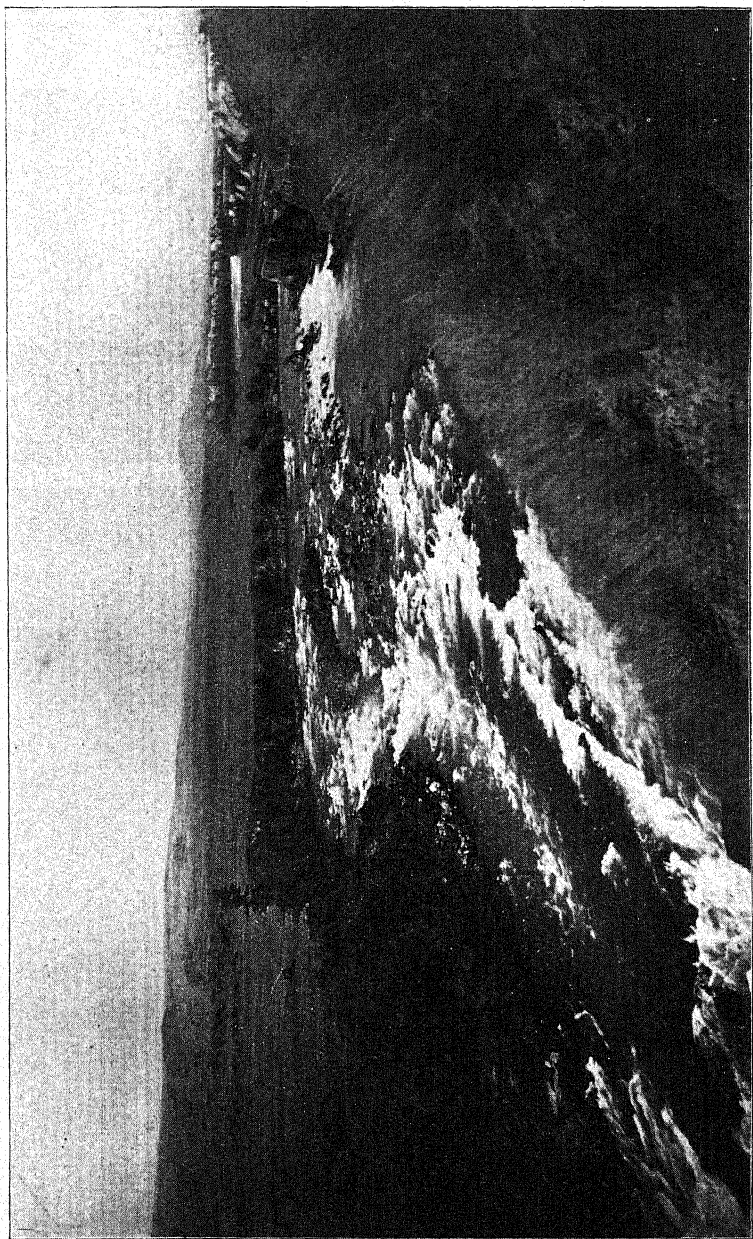


FIG. 6.—Pend d'Oreille River, the present outlet of Flathead Lake; the river has cut through moraine shown in fig. 5; as its channel was eroded the level of the lake was lowered, and the receding waters left broad areas of level land.—From photograph by ELROD.

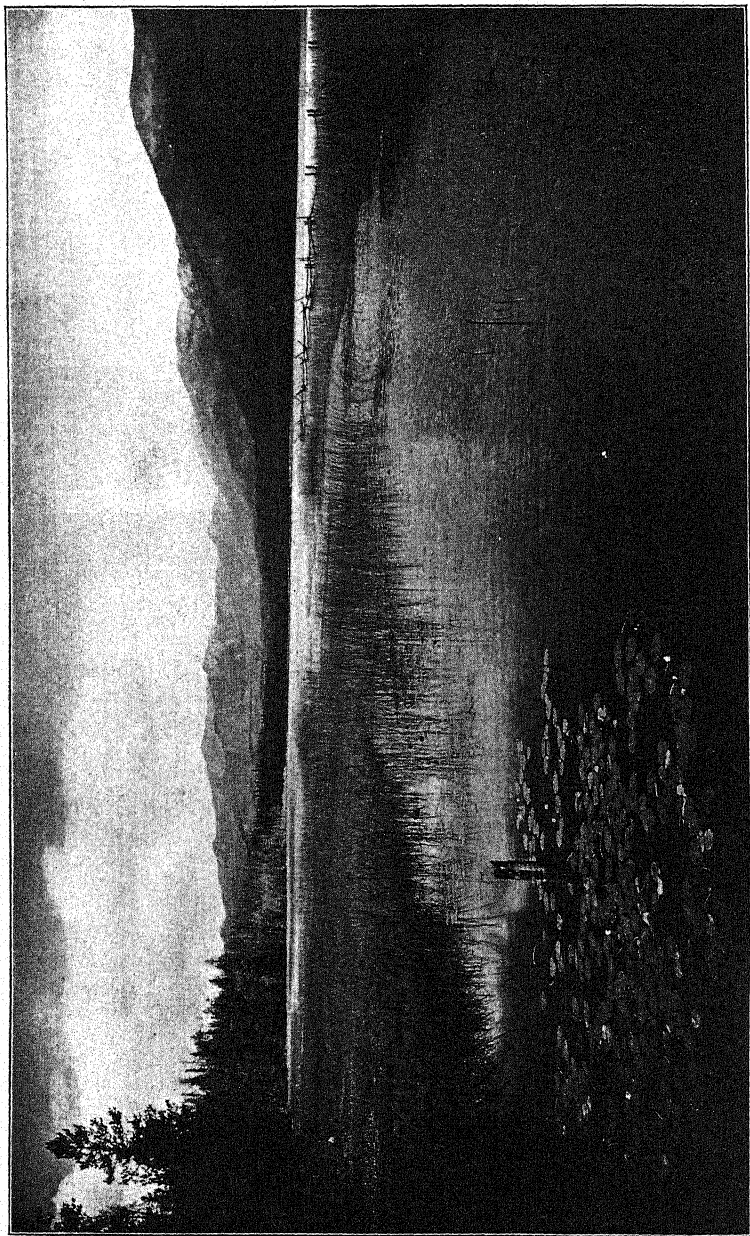


FIG. 7.—Looking north from the south end of Ross Lake; in the deeper waters are *Nuphar advena*, *Brasenia purpurea*, *Polonogeton* sp., etc.; around the borders are sedges and grasses; outside these is the Engelmann spruce formation; the meadow is submerged during the spring and early summer months.

was probably thrown across the mouth of the Swan valley, and thus its connection with the main lake was cut off. A gap in the Mission Range offered a favorable place for the water thus cut off to make its escape. This outlet, of course, marked the beginning of that portion of the Big Fork River known as the "rapids" (*map*). Just as the present condition of the drainage system of Flathead valley is only a stage in the history of the destruction of the former enlarged Flathead Lake, so the existing drainage system of the Swan valley is only a stage in the history of the destruction of the former more extended Swan Lake. This system consists of Swan Lake; its inlet, Swan River; and its outlet, Big Fork River. Swan Lake is a body of water some twelve miles long and, except at its upper end, very narrow. It passes almost imperceptibly into the Big Fork River. This is a meandering stream which with its branches drains the valley and the mountains lying to the east and west of it. With the exception of small rapids here and there, and that part of it known as the "rapids," the river is a rather sluggish stream. The valley (*fig. 8*) is approximately 945<sup>m</sup> above the level of the sea. The Swan Range of the Kootenai Mountains rises abruptly from the east side of the valley to an altitude of from 1800 to 2200<sup>m</sup>, and the Mission Mountains border the valley on the west.

Such, in brief, are the main features of the physiography of the Flathead valley and its arm, the Swan valley. More detailed peculiarities will be noted in connection with the discussion of the edaphic formations; for, as will be shown later, there is an intimate relation existing between the destruction of the two lakes and the development of the plant formations that are found in the valleys.

#### GEOLOGY.

Flathead valley is not, as one would suppose, an erosion valley, but according to WILLIS<sup>7</sup> it is due to a fault resulting in the downthrow of the region of the valley and an uplift of the region of the present Rocky Mountains. The northern Rocky Mountains consist of limestones, quartzites, and siliceous argillites about 2750<sup>m</sup> thick. During pre-Cambrian times the whole was under water. At the beginning of the Cambrian age an uplift brought it above

<sup>7</sup> WILLIS, BAILEY, Structure of the front range, northern Rocky Mountains, Montana. Science N. S. 15:86-87. 1902.



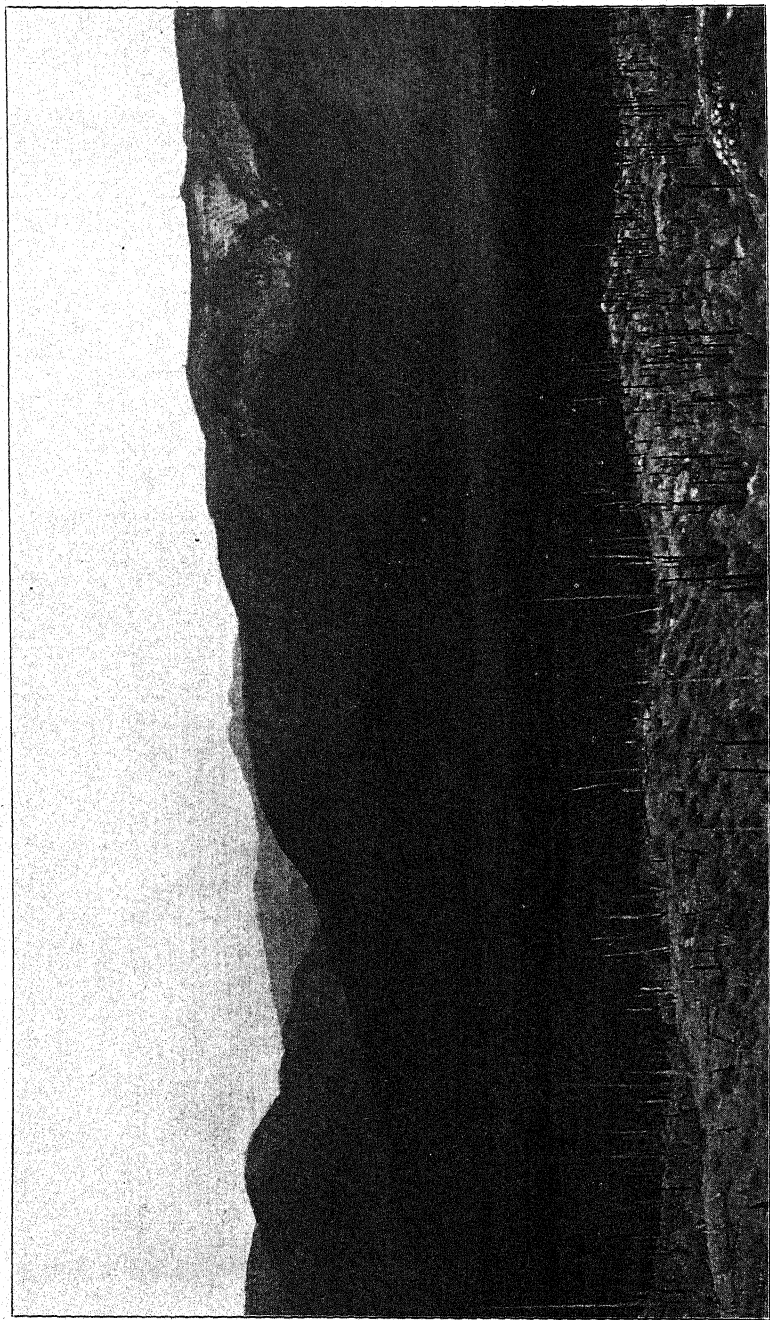


FIG. 8.—General view looking across the Swan valley from Mission Range; Swan Range in the distance; the forest in the valley is western larch-Douglas spruce type except where the lodgepole pine has come in after fires; in the foreground a portion of the Mission Range; the forests completely destroyed by fires.—From photograph by ELROD.

water, and during all the Palaeozoic and part of the Mesozoic the pre-Cambrian rocks were subjected to subaerial erosion. A movement at the close of the Jurassic again brought the sea over it. Then Cretaceous sediments of considerable thickness were deposited upon pre-Cambrian limestone and quartzite. In post-Cretaceous times a fold was overturned to the northeast. Some time in the Tertiary, probably during the Miocene, the faulting mentioned above occurred. The rocks tilt as a rule to the southeast, the northwest fault face of the rocks being very steep.

#### SUMMARY.

1. The Flathead valley is due to a fault, and is technically known as a rift valley.

2. The greater part of it was formerly occupied by a lake.

3. The present drainage system of the valley consists of the Flathead Lake, the Flathead River and its branches, and the Pend d'Oreille River.

4. The Swan River valley, an arm of the Flathead valley, has for its drainage lines the Swan Lake, the Swan River, and the Big Fork River with its branches.

5. These drainage systems are remnants of the former more extensive lake that occupied the valleys.

#### I. CLIMATE OF FLATHEAD VALLEY IN RELATION TO CLIMATIC FORMATIONS.

It has already been shown that the climate determines the general plant formation of a region. It is important, then, that the elements of the climate be analyzed thoroughly, and it should be pointed out at the same time in just what way these elements affect the distribution of plants. In order to obtain a better understanding of the true relation of the forests of this valley, its climate will be compared with that of the northern peninsula of Michigan, where both deciduous and coniferous forests are found; and with that of the Puget Sound region, where the coniferous type of forest reaches its highest development.

There are meteorological reports from two stations in the Flathead valley. These reports, though meager in some particulars, will give a fair idea of the climatic conditions found in a prairie

formation and in a forest formation. The data collected from Kalispell, Montana, cover a period of from four to five years. This station is located in the prairie region of the valley. From a station at Columbia Falls partial meteorological data were obtained that will give an idea of the climate of the forested portion of the valley. Marquette, Michigan, was chosen as the station to represent the climatic conditions of northern Michigan; and Seattle, Washington, will stand fairly well for the kind of climate found in the Puget Sound region.<sup>8</sup>

#### TEMPERATURE.

The following table contains the latitude, longitude, altitude of the stations, the number of years data have been collected, and the mean annual and monthly temperatures (degrees Centigrade) for the four stations.

TABLE I.

Stations	Lat. Long.	Alt.	Years	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Ann'l
Kalispell.....	{ 48° 10' N. 114° 25' W.	904 <sup>m</sup>	5	-4.0	-4.5	1.5	6.0	10.5	14.0	16.5	16.0	11.0	7.0	0.5	-2.0	6.0
Columbia Falls...	{ About same	946	5	-5.0	-4.5	0.0	6.0	11.5	14.0	18.0	14.0	10.0	6.0	0.0	-4.5	5.5
Marquette.....	{ 46° 34' N. 87° 24' W.	224	29	-9.0	-8.5	-5.0	3.0	9.0	15.0	18.0	17.5	13.5	7.0	-0.5	-5.0	5.0
Seattle.....	{ 47° 38' N. 122° 20' W.	1.5	12	5.5	5.5	7.0	10.0	12.5	15.5	17.5	17.5	15.0	10.5	7.0	6.0	11.0

The significance of these figures will be clearer when it is known just how the temperature influences the various physiological processes. An examination of Table I and *fig. 9* will show that the mean monthly temperatures during the growing season is rather low as compared with regions farther south; also, during the months of May, June, July, August, September, the means for the four stations are not far apart; so that any difference in the type of vegetation in the four stations cannot be accounted for by differences in temperature during the so-called growing season. If the temper-

<sup>8</sup> The data given in the tables below were obtained from the following gentlemen in charge of the stations at their respective cities: Kalispell, Mont., H. B. DICK; Marquette, Mich., H. R. PATRICK; Seattle, Wash., G. N. SALISBURY. The figures for Columbia Falls, Mont., were obtained from the Climate and Crop Service Bulletin of Montana for 1900 and 1901. No sunshine records are kept at Marquette, so those from Escanaba, Mich., are taken to represent northern Michigan in that particular.

ature has anything to do with the difference in the character of the vegetation, it must be the temperature of the non-growing rather than of the growing season.

It is too often assumed that during the non-growing season physiological processes of plants are inactive.<sup>9</sup> Of course, this is true of growth; indeed, growth is checked and ceases rather early in the season; but photosynthesis is known to occur during the winter months. Experiments by MIYAKE<sup>10</sup> show that this process is active at temperatures in the neighborhood of 0° C. Among the evergreen leaves experimented upon were species of pine and spruce. One of MIYAKE'S conclusions is that starch is formed in winter, though

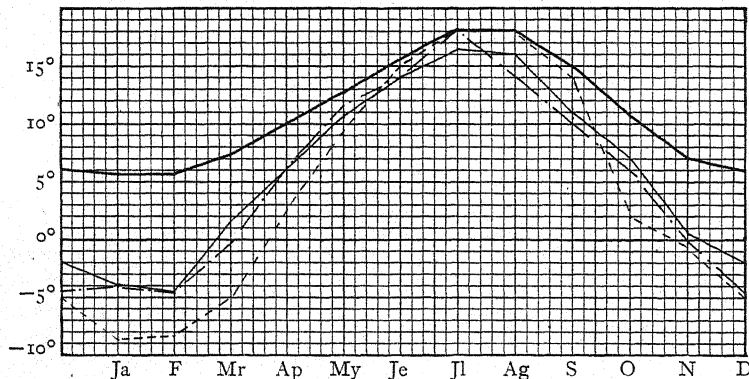


FIG. 9.—Comparative temperature for Seattle (—), Kalispell (— · — · —), Columbia Falls (— · — · —), and Marquette (----); the figures are temperature Centigrade; winter temperature for Seattle comparatively high, for Marquette low, for Kalispell and Columbia Falls intermediate; summer temperature for all stations nearly the same.

in small amounts, and its translocation occurs in the same season. His work was conducted at Tokyo, Japan, where the mean temperature of the three winter months is as follows: December, 5.1° C.; January, 2.7° C.; and February, 3.5° C. If trees can do photosyn-

<sup>9</sup> MERRIAM says that "in computing the sum of the positive or effective temperatures a minimum of 6° C. has been assumed as marking the inception of the period of physiological activity in plants and of reproductive activity in animals." MERRIAM, C. H., Life zones and crop zones of the United States. U. S. Dept. Agric., Div. Biol. Survey, Bull. 10: 4, note 2. 1898.

<sup>10</sup> MIYAKE, K., On the starch of evergreen leaves and its relation to photosynthesis during the winter. BOT. GAZETTE 33:321-340. 1902.

thetic work in the climate of Tokyo during the winter months, it is possible that more food is manufactured by the trees in the Puget Sound region, where the temperature is even higher than at Tokyo. If this be the case for the winter months, it will be even more so for the early spring and late fall months, when the mean temperatures at Seattle are as follows: March,  $7.22^{\circ}\text{C.}$ ; April,  $10^{\circ}\text{C.}$ ; October,  $10.5^{\circ}\text{C.}$ ; and November,  $7^{\circ}\text{C.}$

The evergreen trees, however, in a climate like that at Marquette would not be able to do so much work during these months, for the temperature is very much lower. In other words, in a climate with warm winters like that at Seattle, the evergreen trees can work more or less during the winter, early spring, and late fall months; while in a climate like that at Marquette, where the mean temperature is considerably below the freezing point during the winter months, this work would be very much checked if not stopped altogether. As one would expect, from this standpoint, the conifers would be more successful in the Puget Sound region than in the northern peninsula of Michigan. The conclusion that is reached from the foregoing is that, other things being equal, an equable distribution of heat is favorable to conifers. A reference to the temperature conditions in the Flathead valley will show that the climate is more equable than that at Marquette, but not so equable as that at Seattle. The coniferous forests are better developed here than at Marquette, but are not nearly so luxuriant as at Seattle. From the standpoint of carbohydrate manufacture, the deciduous trees are little or not at all affected by the temperature conditions of the non-growing season, for their leaves are absent, and consequently photosynthetic work is very much reduced.

A comparison of the temperature conditions at Kalispell and Columbia Falls shows a little difference, the latter being slightly colder. While this difference may affect herbaceous vegetation, it would likely have little or no effect on the forests; so the fact that there is no forest at Kalispell, while there is one near Columbia Falls will have to be explained on other than temperature grounds.

Transpiration, which also takes place during the non-growing season, will be discussed in another connection.

## RAINFALL.

The greatest danger to trees is an excessive loss of water, and therefore the rainfall of a region is very important. It will be pointed out later how the conservation of this water supply influences the character of the forest. Other things being equal, the greater the amount of rain that reaches the earth, the more luxuriant the vegetation. The mean monthly and annual rainfall for Kalispell, Columbia Falls, Seattle, and Marquette are as follows, the amounts being given in millimeters:

TABLE II.

Stations	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Ann'l
Kalispell. ....	24	25	16	21	60	47	33	28	50	18	40	35	415
Columbia Falls.....	48	38	36	33	66	72	37	31	68	30	54	30	543
Marquette.....	52	45	47	51	76	80	77	73	99	83	60	62	823
Seattle.....	111	94	79	82	86	40	17	14	45	76	143	158	945

The difference in the amount of rain on the west and east sides of Flathead valley no doubt explains the difference in the types of vegetation in these two situations. It has already been shown that there is only a slight difference in the amount of heat at the two situations. It is very probable that the other elements of climate—light and velocity of wind—are about the same for the two places, although there are no data to prove this. It must be remembered that the towns are only thirteen miles apart, but the difference in rainfall is 128<sup>mm</sup>. It is believed that this difference is sufficient to make a forest vegetation at Columbia Falls and only a prairie vegetation at Kalispell. Kalispell is well out in the valley, while Columbia Falls is at the base of the mountains. The rain-bearing winds from the west sweep across the high mountains west of the valley, where they lose a considerable portion of their moisture, and then descend into the valley where the higher temperature they encounter enables them to hold more moisture. This is liberated, however, when the winds bank up against the cool mountains east of the valley. Thus the west side of the valley probably has a rainfall of 400<sup>mm</sup> or less and is not able to support tree growth except along streams; while the east side has a rainfall of from 400 to 543<sup>mm</sup>, a sufficient quantity

to enable forests to exist. It is very probable that farther to the east in the mountains there is a still greater quantity of rain. At least the character of the vegetation would suggest that this is the case, for here the forest growth approaches in luxuriance that of the Puget Sound region where the rainfall is much greater.

A comparison of the rainfall in the valley with that of the Puget Sound region and of the northern peninsula of Michigan will lead to some interesting conclusions (Table II and *fig. 10*). In this comparison the data at Columbia Falls will be used rather than those at Kalispell, for reasons that are at once apparent. The character of

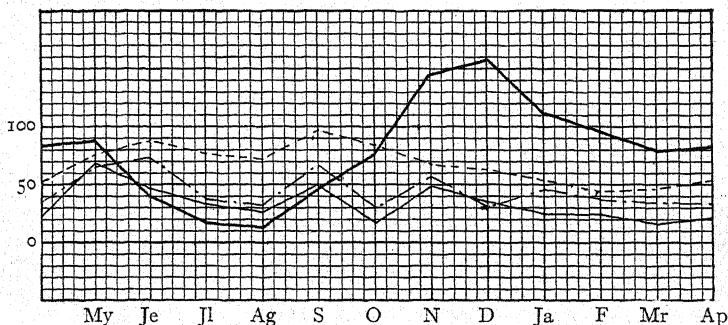


FIG. 10.—Comparative rainfall for Seattle (—), Kalispell (---), Columbia Falls (— · — ·), and Marquette (----); the figures are millimeters of rainfall; summer rainfall highest at Marquette and exceedingly low at Seattle; in winter rainfall the reverse is true.

the distribution of the rainfall is of considerable importance. Thus at Marquette and Columbia Falls the rainfall is more or less evenly distributed throughout the year, with the five warmest months, May, June, July, August, and September, having about half of the moisture. Thus these five months at Columbia Falls show a fall of 274<sup>mm</sup> out of a total of 543<sup>mm</sup>; and at Marquette 414<sup>mm</sup> out of 823<sup>mm</sup>. On the other hand, Seattle with its total of 945<sup>mm</sup> has only 202<sup>mm</sup> during these months. It is a well-known fact that the broad-leaved deciduous trees evaporate more moisture during the summer months than do the narrow needle-like leaves of the conifers. It is very possible that the 202<sup>mm</sup> at Seattle and even the 274<sup>mm</sup> in the Flat-head valley are not sufficient to maintain the broad-leaved deciduous trees in these climates. In any event, they are absent in the two



regions, except along water courses, and are present in the Marquette region where they are more successful than conifers.

The winter distribution of rain is of extreme importance, especially to those trees that hold their leaves, for KUSANO<sup>11</sup> has shown that evergreen leaves transpire considerably even at temperatures below freezing. While there are no data to show whether the bare twigs of deciduous trees transpire more or less than those of conifers, yet *a priori* it is very likely that they give off less moisture, for they have less surface. If this be the case, conifers are more in danger of desiccation during the winter months than deciduous trees; for even though the amount of evaporated moisture is slight, it must be remembered that the ground may be cold or even frozen, and that absorption is thus checked. However, if the rainfall is sufficient and the relative humidity of the atmosphere is high, this danger is less. The figures will show that the winter rainfall of the Puget Sound region is excessive, while that of the Flathead valley and the northern peninsula of Michigan is equal in quantity to the summer rainfall. Conifers exist in all three situations. The extensive rainfall in the winter months at Seattle must be coupled with the fact that the temperature conditions during these and the early spring months are exceedingly favorable to certain physiological processes and account for the almost tropical luxuriance of the trees of that region.

#### RELATIVE HUMIDITY.

The relative humidity of the atmosphere is another factor closely associated with the amount of rainfall. The drier the atmosphere the greater the transpiration. Other things being equal, the nearer relative humidity is to absolute humidity, the less water will the trees give off, and the less danger will there be of their desiccation. The greater the saturation deficit, the greater the danger of losing water. The following table will show the mean monthly deficits of the three stations to be considered. Unfortunately there are no data from Columbia Falls.

The high averages of the saturation deficit for July and August for Kalispell, together with the small rainfall, probably account for the

<sup>11</sup> KUSANO, S., Transpiration of evergreen trees in winter. Jour. Coll. Sci. Tokyo 00:313-366. 1902.



TABLE III.

Stations	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Kalispell.....	16.4	21.2	21.5	30.3	23.1	26.1	44.0	41.2	22.1	25.0	17.6	14.6
Marquette.....	16.5	16.4	19.7	23.7	27.0	27.0	27.6	23.3	22.3	19.8	17.5	17.4
Seattle.....	16.0	20.7	25.0	29.2	28.9	30.9	32.6	29.6	24.5	18.4	15.6	15.5

prairie condition there and on the west side of the Flathead valley. It must be emphasized, however, that the saturation deficit is of great importance only in connection with the amount of water available in the soil. If the ratio of the water obtained by the tree from the soil to that given off is 1:—1, then the tree is in no danger of desiccation; if, however, the ratio is —1:1 or 1:1, the tree is in danger of desiccation. From this it will be seen that if there is in the soil plenty of water that the tree can obtain, there will be tree growth though less luxuriant, even though the saturation deficit is high. This accounts for the existence of trees along streams even in prairie regions.

A comparison of the atmospheric deficits of Marquette and Seattle reinforces what was said concerning the rainfall of these two regions. It will be seen that both have a fairly low atmospheric deficit during the winter months, thus decreasing the possibility of transpiration at a time when the ground is cold. In the Puget Sound region the comparatively high temperature renders greater transpiration more likely than in the Marquette region, but this is offset by the fact that the temperature of the soil is no doubt warm, thus rendering available for absorption some of the great amount of water that reaches the soil in the form of rain during these months.

Again, a comparison of the atmospheric deficit data for the five growing months of the year shows a uniformly higher deficit for Seattle than for Marquette. This coupled with the fact that Marquette has a rainfall of 414<sup>mm</sup> during these months against 202<sup>mm</sup> for Seattle makes deciduous forests possible in the former region, but not in the latter.

#### VELOCITY OF WIND.

Another climatic factor that is likely to play a part in the distribution of the forest is the velocity of the wind. Perhaps the great-

est influence the wind has on trees is to increase the transpiration, and they more than any other form of vegetation are subject to the drying effects of winds. Indeed so important does SCHIMPER (pp. 542-555) think this factor that he considers it influential in bringing about the prairie condition. Below is given the mean monthly and annual wind velocities for the three stations. Again, there are no data for Columbia Falls, but the amount of wind is probably not very different from that at Kalispell. The figures are in kilometers per hour.

TABLE IV.

	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Ann'l
Kalispell.....	7.4	7.7	9.5	10.4	10.0	10.1	10.0	9.6	9.0	8.2	7.2	7.2	8.8
Marquette.....	17.3	16.1	16.7	15.4	16.2	12.6	13.8	14.2	16.2	18.0	17.7	18.0	15.9
Seattle.....	10.3	11.1	10.9	10.4	9.5	9.0	7.6	6.6	7.4	8.0	10.1	10.7	9.3

As shown from these figures, one of the remarkable facts about the Flathead valley is the absence of excessive wind. It is believed that this, coupled with the rather low mean monthly temperature for the summer months, is what makes possible so luxuriant a forest, with a rainfall of about 500<sup>mm</sup>. In passing from the east side of the Rocky Mountains into the Flathead valley, the decrease in the amount of wind is very noticeable. Thus, Kipp on the east side of the Rocky Mountains has a normal rainfall of 512<sup>mm</sup>, yet it has no tree growth. Although there are no data to show that there is more wind here than in Flathead valley, the fact is very apparent to one who has been in the two regions. It is believed that the excessive winds prevent the growth of trees, in spite of the fact that there is a rainfall of about 517<sup>mm</sup>, or nearly as much as at Columbia Falls.

Compared with Marquette the wind velocity of Seattle is low. This would again favor a more luxuriant vegetation in the latter region than in the former.

#### SUNSHINE.

The more light, other things being equal, the more work trees can do. On clear days more food is manufactured than on cloudy days. This process can go on, as has been shown, during the non-growing season when the temperature is not too low, though the

amount of food manufactured then is much less than at higher temperatures. Light is the least variable of all the climatic elements. Possibly for a given altitude and a given latitude the variability is not great enough to have much influence on the kind of vegetation. However, the sunshine data may prove of importance in comparison with other regions. In the table below the mean possible hours of sunshine, which would be the same for a given latitude, and the mean actual hours are given. The observations cover a period of short duration.

TABLE V.

	JANUARY		FEBRUARY		MARCH		APRIL	
	Poss.	Act.	Poss.	Act.	Poss.	Act.	Poss.	Act.
Kalispell.....	276.2	88.2	286.8	111.8	370.1	180.7	410.4	240.2
Escanaba.....	283.1	85.3	290.4	120.5	370.3	129.8	407.0	178.4
Seattle.....	276.2	66	286.8	103.8	370.1	168.6	410.4	205.2

	MAY		JUNE		JULY		AUGUST	
	Poss.	Act.	Poss.	Act.	Poss.	Act.	Poss.	Act.
Kalispell.....	471.3	231.4	479.8	279.6	483.2	364.4	442.5	269.6
Escanaba.....	464.1	163.8	471.7	218.7	475.7	211.5	437.6	230.5
Seattle.....	471.3	226.9	479.8	248.5	483.2	301.7	442.5	257.5

	SEPTEMBER		OCTOBER		NOVEMBER		DECEMBER		ANNUAL	
	Poss.	Act.	Poss.	Act.	Poss.	Act.	Poss.	Act.	Poss.	Act.
Kalispell.....	377.5	202.5	335.8	174.6	278.0	73	262.1	49	4473.7	2262.9
Escanaba.....	376.1	149.1	338.5	148.8	284.1	52.9	269.6	61.4	....	1727.1
Seattle.....	377.5	186	335.8	110	278	40.6	262.1	45	4473.7	1959.6

In his classification of climatic formations, SCHIMPER (pp. 556-565) does not recognize a distinct formation for the coniferous forest, placing it in what he calls the summer-green forest (deciduous). There is little doubt that he is right so far as the eastern part of the United States south of the latitude of Lake Superior is concerned. Here, as shown by COWLES (*l. c.*) and the writer (*l. c.*), the conifer-

ous forests occur as edaphic formations in the summer-green climatic formation. In this region they are xerophytic formations (societies) forming a stage in the progression toward the climax mesophytic deciduous forest formation. With the wearing down of the xerophytic hills, the filling up of swamps, and the accumulation of humus on the sandy plains and hills, the coniferous societies which now prevail there will give way to the climax deciduous forest, which is the highest expression of a climate similar to that found in the eastern United States.<sup>12</sup>

The Pacific coast district north of San Francisco, and including the moister mountainous regions inland, presents a climate entirely different from that of the eastern United States. Here, as compared with the eastern deciduous forest region, there is a more equable distribution of temperature throughout the year, with winter rains and excessively dry summers. The forests here are coniferous, with the deciduous element occupying only edaphic situations along water courses. It is my belief that in some such climate as that found in the Puget Sound region the coniferous forest is at its best, the deciduous type being unable to compete with it because of the dry summers.

The climate and character of the vegetation of the Pacific coast region corresponds more nearly with SCHIMPER'S sclerophyllous woodland (pp. 464-469, 507-540) than they do with his summer-green climate and vegetation. Indeed, elements of the sclerophyllous vegetation are found in the Puget Sound district, for here such trees as *Arbutus Menziesii* show a type of leaf decidedly like that found in climatic districts which SCHIMPER has so aptly called sclerophyllous woodlands. The sclerophyllous formations are in a climate with winter rain and comparatively high and equable temperature. Likewise the Pacific coniferous district has winter rains and a comparatively equable temperature, that is rather warm winters and cool summers. However, the mean average monthly temperature is much lower than that of the sclerophyllous districts of the warm temperature belt. This is no doubt influential in bringing about the narrow type of evergreen leaf rather than the broad type found in the warmer climate.

<sup>12</sup> See SCHIMPER (p. 545) for table showing rainfall of Atlantic forest district and Pacific coast.

For reasons given above, it is my belief that SCHIMPER's summer-green climatic formation should not include the coniferous forests of the Pacific coast of North America, but that these should be separated from it. In order to show its relations to the broad-leaved sclerophyllous formation, I would suggest that it be called the *needle-leaved sclerophyllous formation*. The limits of this formation are not clear. While no doubt it reaches its best development in the Puget Sound region, this does not prevent its spreading into more northerly regions with cooler but still damp winters. Whether this type is the climax forest formation in the region north of the Lake Superior district, as it is on the Pacific coast, or only edaphic formations in the summer-green climatic formation of the United States, our present knowledge cannot determine.

The forests of the Flathead valley clearly belong to the needle-leaved sclerophyllous formation, but since they are on the border of a prairie climate they are not so good an expression of it as is that of the district farther west.

[To be continued]

## STUDIES IN THE GRAMINEAE.

### VIII. MUNROA SQUARROSA (NUTT.) TORR.<sup>1</sup>

THEO. HOLM.

(WITH TWELVE FIGURES)

It often happens that plants which are common and easily available are the least studied. Being frequently collected and represented in herbaria by almost numberless specimens, such plants become so familiar "by name" that botanists as a rule do not take the pains to examine them with much interest or care.

The steady increase in the publication of cheap systematic works in this country is hardly beneficial to the study of taxonomic botany. The danger lies in the fact that authors of such works seldom take the time to reexamine the plants or to compare them with diagnoses of earlier date. It is no surprise, therefore, to discover points of great importance mentioned in earlier diagnoses which have been totally overlooked or ignored in works of a more recent date. As a matter of fact, the older botanists were more careful in examining and describing their plants, and their diagnoses, brief as they may be, often allude to certain characters which are well worthy of notice. A case in point may be illustrated by *Munroa*, and in selecting this genus as the subject of the present paper, it is with the intention of showing that the plant was actually better understood formerly than it is now, and that it possesses certain morphological and histological characters which have not been observed hitherto and which may be of some importance to future research.

*Munroa* was first described as a species of *Crypsis*—*C. squarrosa*—by NUTTALL, but TORREY corrected the mistake and established the genus.<sup>2</sup> At that time it was considered as belonging to the HORDEAE, while it is now generally placed among the FESTUCEAE. As described by TORREY, the plant is readily recognized, and both the singular

<sup>1</sup> Earlier papers were published in this journal as follows: I, June 1891; II, August, 1891; III, October 1891; IV, November 1892; V, August 1895; VI, June 1896; VII, November 1896.

<sup>2</sup> Pacific R. R. Rep. 4:158. 1856.

habit and the inflorescence are exceedingly well characterized. There is one point especially which has escaped the attention of later botanists, namely, that the spikelets are dimorphic in respect to the shape of the glumes. It is true that TORREY did not express this as plainly as he might have done, but his diagnosis certainly shows that he did observe the different structure of the spikelets, as shown by the following statement: "In the uppermost spikelet, and often in the middle one, these nerves are bearded with long white hairs towards the base; but the flowers of the lowest spikelet are usually quite naked." That BENTHAM and HOOKER considered this character of some importance is evident from their description of the flowering glumes as being "longe ciliatis v. in eodem fasciculo glabris."<sup>3</sup> But none of the subsequent authors, not even the agrostologists, appear to have noticed this point, and it so happens that the genus has been received as a plant of rather ordinary habit, distinct from *Monanthochloe* by "Spikelets usually in threes, terminal in the axils of stiff spinescent leaves which project far beyond them."<sup>4</sup>

Since TORREY called attention to this slight modification in structure of the flowering glumes, it seemed natural to investigate the matter further, as it might lead to the discovery of additional characters sufficient to attribute a certain degree of dimorphism to the spikelets. A careful examination of a large number of specimens, studied in the field, revealed the fact that *Munroa* does exhibit such dimorphism constantly, and to a greater extent than hitherto observed. The deviation is not only due to the presence of long white hairs at the base of the flowering glume in the uppermost spikelet in contrast with the others, as first described, but the complete structure of these spikelets is quite prominently distinct. As a rule, each inflorescence (*fig. 1*) in *Munroa* consists mostly of three spikelets, one median and two lateral; and when only two are developed, one of them shows always the structure of a median and the other that of a lateral spikelet. Of the two spikelets here figured, *fig. 2* represents the median and *fig. 3* one of the two lateral. It is readily seen from the drawings that the structure of these spikelets is distinct. The empty glumes are very unequal (*figs. 2* and *4*) in the median, but

<sup>3</sup> *Genera plantarum* 3:1180. 1883.

<sup>4</sup> SCRIBNER and SOUTHWORTH, *The true grasses*. New York. 137. 1890.

almost equal in the lateral spikelets (fig. 3); the flowering glume is pubescent in both, but in the median there are three distinct nerves with a tuft of long hairs at the base (figs. 2, 5, and 6), while in the lateral the nerves are not visible, and no long hairs are developed (figs. 3 and 7); moreover, the apex of the flowering glume is long-awned and distinctly bidentate in the median (figs. 5 and 6), but merely emarginate and short-awned in the lateral spikelets (fig. 7). Some distinction in regard to texture is also observable, the flowering glume

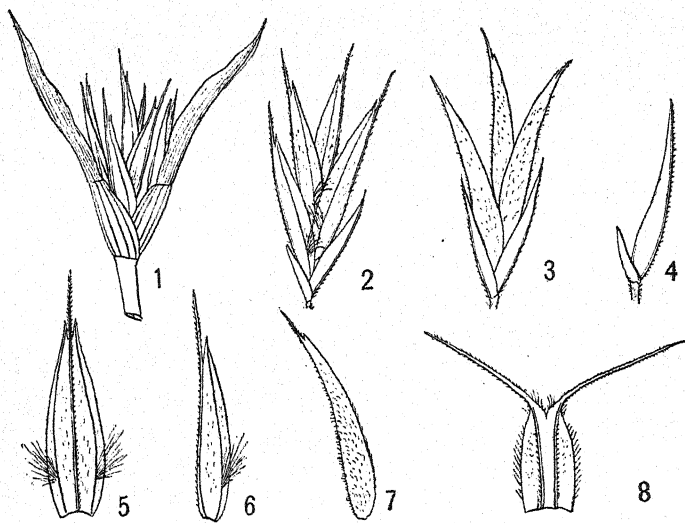


FIG. 1.—*Munroa squarrosa*.—The inflorescence, magnified. FIG. 2.—A terminal spikelet. FIG. 3.—A lateral spikelet. FIG. 4.—The empty glumes of a terminal spikelet. FIG. 5.—Flowering glume of same, dorsal view. FIG. 6.—Same, side view. FIG. 7.—Flowering glume of lateral spikelet, side view. FIG. 8.—The prophyllon, dorsal view.

and the palea being membranaceous in the median, but quite thick and coriaceous in the lateral spikelets. It may seem justifiable, therefore, to consider the spikelets of *Munroa* as being dimorphic, even if we have not been able to observe any deviation in regard to the distribution of the sexes within them.

While TORREY's description of the spikelets contains a good deal more than is recorded by subsequent writers, except BENTHAM and HOOKER, there are some other points which may be added to the diagnosis of this singular grass. The mode of growth is very well



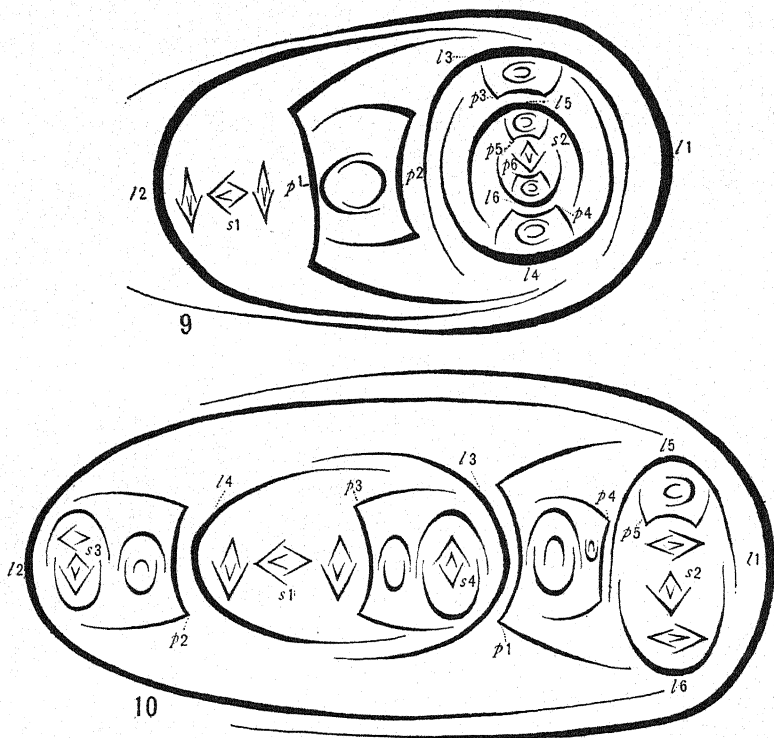
characterized by TORREY, but there are some peculiarities which have been omitted, and these consist especially in the structure of the shoots, the vegetative and the floral; furthermore, the histology has only been touched upon very briefly.

The peculiar bushy habit of the plant depends upon the fact that the culms are not directly terminated by the inflorescence. Usually in the Gramineae the long internode of the culm passes immediately over into the inflorescence, but in *Munroa* the spikelets are preceded by two or three green leaves which are borne upon the culm near the apex, and whose internodes are exceedingly short, often being barely visible. These green leaves all subtend shoots, which develop into floral or vegetative branches, and quite often into secondary culms from the apex of which the same development of shoots is repeated. Beneath the terminal inflorescence there is thus a small cluster of shoots, developed in the axils of green leaves, a ramification that calls to mind the well-known condition known in teratology as "prolification," but which is normal and constant in *Munroa*. To separate these shoots and to define their proper order might at first glance seem difficult, not only on account of their relatively large number, but also because the internodes are so very short. However, if we examine the shoots carefully, it is easily seen that the first leaf of several of them represents a fore-leaf (prophyllon) of most characteristic and striking shape.<sup>5</sup> The presence of a fore-leaf actually gives the clue to the composition of these "fascicles of leaves and shoots," since it always signifies a lateral ramification, and in the Gramineae is nearly always situated on the branch with its dorsal surface toward the mother axis. In *Munroa* this prophyllon has attained a high development, and is not only represented by an open sheath-like body, but the two nerves are extended into very long, stiff, divergent setae (*fig. 8*); the sheath-like portion is membranaceous, ciliate, and minutely pubescent on the dorsal face. Altogether it is a structure so remarkable and characteristic that it may well deserve to be mentioned in the diagnosis of the genus.

The composition of the shoots in *Munroa* is illustrated by the two accompanying diagrams (*figs. 9 and 10*), which represent two fre-

<sup>5</sup> Some new anatomical characters for certain Gramineae. Beihefte Bot. Cent. 11:28. 1901.

quent instances of ramification. In these diagrams  $L^1$ ,  $L^2$ , etc., all represent assimilating leaves with sheaths and blades developed as ordinary grass leaves, and they differ in no respect from the others which are situated at the base of the culms, where they form a dense rosette. On the other hand,  $P^1$ ,  $P^2$ , etc., are prophylla or



FIGS. 9 and 10.—*Munroa squarrosa*. Diagrams of two fascicles of shoots from the apex of two culms:  $l$ , the green leaves;  $p$ , the fore-leaves;  $s$ , the spikelets; for further explanation see text.

fore-leaves, and their form as indicated is almost like their cross-section. Thus their actual position may be readily understood, the concave side (dorsal) turning toward the mother axis.  $S^1$ ,  $S^2$ , etc., are the spikelets, of which only the empty glumes and one of the flowering have been drawn, in order to show the mutual position of the spikelets—median and lateral—and of their respective glumes.

In fig. 9 the two leaves  $L^1$  and  $L^2$  are developed a very short dis-

tance below the inflorescence ( $S^1$ ), which terminates the culm of the main stem; they are exactly alternate, and so are the glumes of the median spikelet ( $S^2$ ); in the two lateral the same position is noticeable, but these have been turned so as to form an angle of  $90^\circ$  with the median, the terminal spikelet. In the axil of  $L^1$  a complex of shoots may be seen, beginning with a prophyllon ( $P^1$ ) with its back toward the main axis, but alternating with the leaf  $L^1$ . The subsequent leaves ( $L^3$ – $L^6$ ) of this axillary shoot, on the other hand, are turned  $90^\circ$  to the side of the leaf  $L^1$ , but are otherwise alternate. The first of these leaves ( $L^3$ ) supports a bud with a prophyllon and two small leaves, and similar buds are also observable in the axils of the other leaves ( $L^4$ – $L^6$ ). The apex of the whole shoot terminates in a single spikelet ( $S^2$ ), the arrangement of whose glumes, alternating with the green leaves of the same axis, shows that it is a median and not one of the lateral spikelets; these have become suppressed entirely in this instance.

There is still another shoot observable, however, namely the one whose prophyllon is marked  $P^2$ , and which has only two green leaves. This little shoot comes from the axil of the large prophyllon  $P^1$ , Munroa thus illustrating a case, not unusual among Gramineae, in which prophylla may subtend shoots. It is furthermore noticeable that this prophyllon ( $P^2$ ) and the leaves of its shoot lie distinctly in the same plane as the first leaves ( $L^1$  and  $L^2$ ) and the first prophyllon ( $P^1$ ). In this way the spikelet  $S^1$  terminates the main culm, while the other ( $S^2$ ) terminates the shoot developed from the axil of the leaf  $L^1$ .

The succession of these various leaves ( $L$  and  $P$ ) seems invariably the same, inasmuch as no instance was observed where the inflorescence was directly preceded by a prophyllon alone. But the number of vegetative shoots in Munroa is sometimes much larger than that of the floral, and the reason seems to be, at least judging from this particular instance (*fig. 9*), that the shoots were so crowded within the leaf axil that the development of flowers became arrested. This explanation may seem justifiable when we examine the other diagram (*fig. 10*), which shows a more balanced growth of the whole system of axes, instead of the one-sided development of shoots shown in the former diagram (*fig. 9*), where no axillary branch was developed from the leaf  $L^2$ , but only from  $L^1$ .

In *fig. 10* there are represented four inflorescences and five vegetative shoots, but much more equally distributed than before, since the main culm bears here a larger number of leaves—four instead of two—three of which ( $L^1$ – $L^3$ ) subtend shoots. These leaves ( $L^1$ – $L^4$ ) are also exactly alternate and lie in one plane, and the uppermost ( $L^4$ ) precedes an inflorescence ( $S^1$ ) which terminates the main culm. Similar to the specimen illustrated in *fig. 9*, the first leaf ( $L^1$ ) subtends a shoot with a large prophyllon ( $P^1$ ), and this shoot is also turned  $90^\circ$  to the side of the supporting leaf and the prophyllon; but it bears only two leaves ( $L^5$  and  $L^6$ ), one of which ( $L^5$ ) has an axillary shoot consisting of a prophyllon and a vegetative apex. The other leaf ( $L^6$ ) has no shoot and precedes the terminal inflorescence ( $S^2$ ) of three spikelets, arranged in conformity with the leaves ( $L^5$  and  $L^6$ ). Another shoot is observable in the axil of the large prophyllon  $P^1$ , which shows the same development as the one in *fig. 9*, but with the exception that an axillary shoot is visible within the prophyllon ( $P^4$ ); thus two prophylla of the shoot-complex pertaining to leaf  $L^1$  support buds.

Examining the other shoots, we find one in the axil of leaf  $L^2$  with a prophyllon ( $P^2$ ), whose leaves and inflorescence are likewise turned  $90^\circ$  to the side, with exception of the prophyllon. This shoot consists of a terminal portion with two leaves and a two-flowered inflorescence ( $S^3$ ; one median and one lateral spikelet), besides a secondary, purely vegetative bud which is developed in the axil of the prophyllon, but although axillary its prophyllon has become suppressed. The position of the floral shoot, however, shows clearly that it is terminal, and that the other much smaller one must belong to the prophyllon. A similar construction of two shoots pertaining to one system is to be found in the axil of the leaf  $L^3$ , where we observe the same position of the prophyllon ( $P^3$ ) and of the green leaves as before. The shoot bears two leaves and is terminated by a single spikelet ( $S^4$ ), which shows the arrangement of the glumes as that of a median rather than of a lateral spikelet, since the glumes alternate with the leaves. It is now interesting to see that the prophyllon ( $P^3$ ) here also subtends a bud, and a purely vegetative one. The fourth leaf ( $L^4$ ) has no bud and precedes directly the inflorescence ( $S^1$ ), which terminates the main culm; thus the median spikelet represents

the uppermost terminus, and its glumes are situated so as to alternate with the four leaves ( $L^1-L^4$ ) borne on the culm.

Such is the usual composition of the fasciculate shoots in *Munroa squarrosa*, but there are of course many variations in proportion to the number of shoots developed. However, the succession of leaves appears constant, and the modification by suppression of some of the spikelets or of the vegetative shoots does not influence the principal structure as described above. It is a structure which no doubt is uncommon among the Gramineae, even if the components of the shoots may be identical. Somewhat similar and equally complicated cases of ramification may be observed in Coix, in Andropogon, and especially in Jouvea. North American Gramineae exhibit altogether a number of types in regard to inflorescence and ramification of axes which are very little known and which deserve attention. In *Munroa* the most striking peculiarity depends, as stated above, upon the presence of short internodes with green leaves above the longest internode of the culm, preceding the terminal inflorescence. Furthermore, it is characterized by the profuse development of shoots, floral and vegetative, from the axils of these leaves; and also by the elongation of some of these into secondary culms, at the apex of which the same development of fasciculate shoots occurs.

From a morphological aspect, therefore, *Munroa squarrosa* offers several important characters, but it exhibits also some points of histological interest, which may be mentioned in this connection. As an inhabitant of the arid plains, it would be expected that our plant would possess a xerophytic structure, which it does; but such structure is far from common among its associates. Ecological studies are very seldom extended beyond the mere fact that such and such plants constitute associations; whether the external and internal structure of such xerophytes, for instance, is in real harmony with the surroundings is very seldom touched upon. The xerophytic characters have been very excellently defined by several prominent authors, by WARMING and SCHIMPER for instance; but whether these characters are to be observed in all the members of such xerophilous associations remains to be seen. It would require an immense amount of work, and nothing more or less than a complete investigation of the internal structure of desert plants. Very few

of our plants have been studied from this particular point of view, and the following notes on the histology of *Munroa squarrosa* may be regarded, therefore, as a small contribution towards the knowledge of this interesting plant association. With this object in view, the writer has examined the structure of the roots, the culm, the proper leaves, and the prophyllon, and finally the flowering glumes of both forms of spikelets.

**THE ROOTS.**—The roots are thin, hairy, not very strong, relatively short, and but little ramified. In a mature root the epidermis and the moderately thick-walled hypoderm persist, but the cortex,

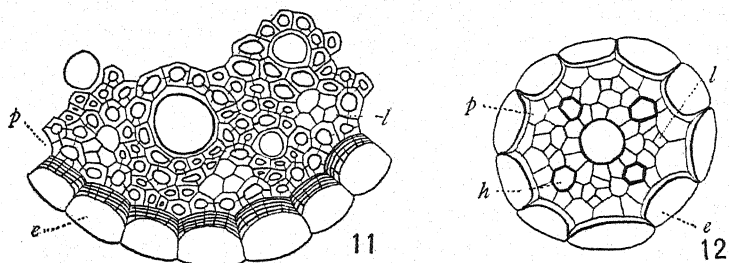


FIG. 11.—*Munroa squarrosa*.—Transverse section of a mature root: *e*, endodermis; *p*, pericambium; *l*, leptome.  $\times 560$ . FIG. 12.—Transverse section of a capillary lateral root: *h*, proto-hadrome; the other letters as above.  $\times 560$ .

which consists of only three or four layers, collapses radially. The inner walls of the endodermis (*fig. 11, e*) are considerably thickened with distinct layers and pores; and it surrounds a pericambium which is thickened throughout. Therefore the location of the proto-hadrome vessels could not be clearly ascertained, and the inner portion of the central cylinder is occupied by a mass of thick-walled conjunctive tissue with about ten broad rays of hadrome. The leptome constitutes very small groups, when viewed in transverse sections (*fig. 11, l*). A younger stage of the root shows these same elements much less thick-walled. Thus it was possible to distinguish the pericambium cells from the proto-hadrome vessels, and it was noticed that the latter had penetrated the pericambium in all places. If one of the capillary lateral roots (*fig. 12*) is examined the same structure is observed, but the center of the root is here occupied by a large vessel, and the hadromatic rays are merely represented by four proto-hadrome vessels (*fig. 12, h*), all of which are located inside the peri-

cambium. We do not attach much importance to this varied position of the proto-hadrome, however, since we have ascertained that it is not constant, a fact that has been recorded in some previously published papers.<sup>6</sup> A characteristic of the root of *Munroa* seems to be the poorly developed cortex in contrast with the prominent and thick-walled inner tissues of the central cylinder.

**THE CULM.**—The long internode is semicylindric, smooth, and almost glabrous at the base; but cylindric, deeply furrowed, and scabrous above. The smooth and quite thick cuticle covers a very small-celled epidermis, whose outer walls are prominently thickened. Stomata are frequently near the furrows of the upper part of the culm, and their guard cells are level with the epidermis. Unicellular, pointed projections abound along the elevated ridges, but decrease in number toward the base, where the surface of the culm is smooth. The cortical parenchyma is well differentiated in the upper part, where it occurs as a single layer of palisade cells, filled with chlorophyll, and bordering on the parenchyma sheath of the peripheral mestome bundles; the palisades are very regularly arranged, radiating from the parenchyma sheath. Another tissue of about five layers, but composed of colorless, more roundish cells, occupies the space between the peripheral mestome bundles with their covering of palisades, and this tissue belongs also to the cortex. It is developed to a somewhat larger extent at the base of the culm, where no palisades were observed; thus the cortex consists here of a continuous ring of colorless tissue surrounding the mestome bundles.

The mechanical tissue as stereome is well represented and forms sub-epidermal groups in the ridges, bordering on the palisades, besides occurring as a solid, continuous zone all around the inner mestome bundles. Toward the base of the culm the stereome does not occur as sub-epidermal layers, but only as a heavy ring inside the cortex and surrounding both the outer and inner circle of mestome bundles. Throughout the culm there are thus two almost concentric circles of mestome bundles, the peripheral ones being the smaller, orbicular in transverse section, and containing mostly leptome alone; while the larger inner ones are oval and contain both

<sup>6</sup> Compare: *Eriocaulon decangulare* L. BOT. GAZETTE 31:17. 1901; and Studies in the Cyperaceae. XIV. Amer. Jour. Sci. 10:278. 1900.

leptome and hadrome. Common to both is a thick-walled mestome sheath, but the parenchyma sheath is developed only on the outer face of the peripheral bundles, thus bordering on the palisades, being quite large-celled and containing chlorophyll of a somewhat bluish-green color. This parenchyma sheath is thus restricted to this particular portion of the peripheral mestome bundles in the upper part of the culm, where palisades occur, and is entirely absent in all the others. The inner portion of the culm is occupied by a thin-walled pith, which is broken in the center.

Characteristic features of the culm, therefore, are the small development of chlorophyll-bearing parenchyma in the shape of palisades and as an incomplete parenchyma sheath, and the predominating chlorophyll-less cortical parenchyma which evidently has the function of storing water. The stereome is well represented, being thick-walled and constituting heavy layers both in the ridges and inside the cortex.

**THE LEAF.**—The leaf blade is furrowed on both faces, deepest on the ventral, and covered with small obtuse papillae and somewhat larger prickly-like projections like those observed on the culm. The midrib is hardly larger than the other nerves, the blade thus being nearly flat and of the same thickness throughout. Stomata occur on both faces of the blade along the sides of the furrows, their guard cells being level with epidermis. While the cells of epidermis are small and quite thick-walled on the dorsal face of the leaf, those of the ventral are larger and developed as bulliform cells in the furrows between the mestome bundles.

The parenchymatic tissues of the leaf consist of a colorless water-storage tissue, which is located in the furrows beneath the bulliform cells, and consisting of three or four strata. There is also a chlorophyll-bearing tissue, developed as one layer of palisades surrounding the mestome bundles and radiating from them. Similar palisade cells were also noticeable in the upper portion of the culm, and bordering on the incomplete parenchyma sheath.

The mestome bundles are all orbicular in transverse section, and possess a complete green parenchyma sheath besides a mestome sheath, which is somewhat thick-walled in the larger bundles. The leptome and hadrome are well differentiated in all the nerves, espe-



cially in the larger ones. In regard to the mechanical tissue, a stereome occurs in large groups, one in each margin of the blade, besides smaller groups accompanying the nerves, and located above and below them between epidermis and palisades.

Characteristic of *Munroa* and several of its associates among the Gramineae are the nearly orbicular mestome bundles surrounded by the single layer of straight-walled palisades, radiating from them and bordering on a rather large-celled parenchyma sheath, inside of which a typical mestome sheath occurs; and also the deeply furrowed blade with bands of bulliform cells covering strata of colorless tissue, the function of which is evidently to store water. The numerous epidermal projections in the shape of papillae or long-pointed spines partly surround and cover the stomata.

**THE PROPHYLLON.**—This very characteristic leaf, as stated above, consists of a sheath-like, bicarinate, membranaceous body and two long setae, the nerves being extended beyond the apex of the leaf. The structure of the sheath-like portion is very simple, since the margins and the central part possess only an epidermis (the dorsal) with a few stereomatic cells scattered here and there. The two keels, in which two mestome bundles are located, show a more solid structure, since each keel has a support of quite thick-walled stereome, which borders on a large-celled, colorless parenchyma. Each mestome bundle has a closed parenchyma sheath and a moderately thickened mestome sheath. The awns contain chlorophyll, located in a stratum of palisades and in the parenchyma sheath, and stomata occur on the upper surface. A cross-section of one of these awns is sharply triangular, with the two lateral angles occupied by stereome, while the keel contains a large mass of colorless parenchyma. The mestome bundle is located in the center, but is very small and consists only of leptome.

**THE FLOWERING GLUMES AND THE PALETS.**—As stated above, the glumes of the terminal spikelet are somewhat different from those of the lateral in regard to shape and texture, and therefore the spikelets may be designated as "dimorphic." This distinction, however, seems much more pronounced when the internal structure is compared. The empty glumes of both spikelets possess the same structure, even if their form be distinct; but the flowering glumes and the

palets exhibit a structure so distinct that when detached the spikelets may be easily assorted into terminal or lateral by their tissues alone. In the terminal spikelet the flowering glume and the palet are thin and membranaceous, as in the majority of Gramineae. The flowering glume has four prominent ribs on the dorsal face supported by heavy groups of stereome, and small scattered groups of this same tissue are observable also on the ventral face of the glume, but only between the two innermost mestome bundles. Otherwise the glume consists only of a single layer throughout, represented by the dorsal epidermis. The palet of this same spikelet—the terminal—is two-nerved, but very slightly bicarinate, and the structure is even more delicate than that of the flowering glume.

In the flowering glume of the lateral spikelets the structure is very different, a large mass of very thick-walled stereome covering nearly the whole ventral face of the glume, and a colorless parenchyma occupying the larger inner portion. The four mestome bundles are imbedded in this tissue, thus forming no prominent ribs, as is the case in the terminal spikelet. A similar broad stereomatic tissue is observable in the palet on the ventral face, besides a colorless tissue nearer the dorsal. The two nerves are located in this tissue, which extends into two sharp keels with numerous epidermal projections.

So great a diversity in structure observable in the glumes of spikelets belonging to the same inflorescence is evidently very rare within the order. It seems the more peculiar since the spikelets are otherwise identical, the number of glumes being the same, and the flowers perfect in both the terminal and lateral spikelets. The very firm structure, described above, which is especially marked by the unusual development of stereome, is also known in other genera. We might mention, for instance, the coriaceous or cartilaginous empty glumes in *MAYDEAE* and *ZOYSIEAE*; the cartilaginous flowering glume and palet in *PANICEAE* and *ORYZAE*; finally the prominent structural deviation noticeable in the unisexual spikelets of *Buchloe* and *Amphicarpum*. But none of these cases are really comparable with that of *Munroa*, where the only distinction between the spikelets depends upon position, terminal or lateral, and not upon the distribution of sexes, and still exhibiting such marked modification in structure.

The systematic position of *Munroa* seems naturally to be within FESTUCEAE, but it is difficult to place it near any of the genera so as to demonstrate its nearest affinity. Most frequently *Munroa* is placed next to *Monanthochloe*, a genus to which it certainly shows no affinities whatsoever. The peculiarity of the genus seems to depend upon the dimorphism of the spikelets, and to some extent upon the profuse development of shoots, especially vegetative, in the axils of leaves near the apex of the culm, a structure which is exceedingly common in teratological cases, but which is normal and constant in *Munroa squarrosa*.

There may exist some analogous cases, and normally so, among the other members of the order in this country, but so far as known to the writer no investigations have been published dealing with such morphological peculiarities.

BROOKLAND, D. C.

# ALTERNATION OF GENERATIONS IN ANIMALS FROM A BOTANICAL STANDPOINT.<sup>1</sup>

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY.  
LXVIII.

CHARLES J. CHAMBERLAIN

(WITH TWO FIGURES)

SINCE zoologists do not recognize in animals an alternation of generations comparable with the alternation of gametophytic and sporophytic generations in plants, it may seem presumptuous for a botanist to propose any theories. Nevertheless, after hesitating for several years I have decided to publish my belief that animals exhibit an alternation of generations comparable with the alternation so well known in plants.

In short, the theory is this: the egg with the three polar bodies constitutes a generation comparable with the female gametophyte in plants; similarly, the primary spermatocyte with the four spermatozoa constitute a generation comparable with the male gametophyte in plants. All other cells of the animal constitute a generation comparable with the sporophytic generation in plants, the fertilized egg being the first cell of this series.

In support of this theory I shall present two lines of evidence: (1) the gradual reduction of the gametophyte in plants, with the constantly diminishing interval between the reduction of chromosomes and the process of fertilization; and (2) the phenomena of chromatin reduction in both animals and plants.

1. EVIDENCE FROM THE REDUCTION OF THE GAMETOPHYTE IN PLANTS.—For convenience, the female and the male gametophyte will be considered separately. Further, since dioecism in gametophytes is regarded as a more specialized condition than monoecism, and since the tendency is toward dioecism, all cases in which the gametophytes have not attained the dioecious condition may be disregarded.

<sup>1</sup> Presented before Section G of the A. A. A. S., at the Philadelphia meeting, December 30, 1904.

(1) *The female gametophyte*.—In the liverworts the gametophyte is a green, independent plant. It is the conspicuous generation, the sporophyte being comparatively small and never entirely independent. Here the gametophyte generation, beginning with the spore mother-cell and extending to the fertilization of the egg, is a complex plant, of which the egg, the culmination of the gametophyte, constitutes only a very small part. In the mosses the disparity between the gametophytic and sporophytic generations is not so marked, but the gametophyte is still predominant and independent, while the sporophyte never becomes entirely independent. In the ferns the sporophyte has become the conspicuous, independent generation, and the gametophyte is much reduced. In most cases the gametophyte is still a green independent plant, although it is so small that it is likely to be overlooked by the layman. In the heterosporous forms the gametophyte is still smaller, develops little or no chlorophyll, and shows but little differentiation. Compared with the liverworts or mosses, or even with the homosporous ferns, the interval between the reduction of chromosomes and the fertilization of the egg has been immensely reduced.

In the gymnosperms the gametophyte is entirely dependent, being parasitic in the sporophyte at all stages of its development. Although there is a more or less prolonged period of nuclear division before cell walls are formed, the ancestors of these gametophytes were doubtless cellular from the beginning of their development. In *Gnetum* *Gnemon*, cell walls are formed only in the lower portion of the gametophyte, in the upper portion the nuclei lying free in a common layer of cytoplasm. Any one of the free nuclei of the upper portion seems capable of functioning as an egg nucleus. In other species of the same genus no walls are formed even in the lower portion, all the nuclei lying free in the general cytoplasm. In the angiosperms, both the conditions shown by the genus *Gnetum* are found, but reduction has proceeded much farther. A considerable tissue is formed in the lower portion of the gametophyte in *Sparganium*, in the grasses, and to a less extent in some *Compositae* and other forms; the tendency, however, is toward the free nuclear condition already reached by the latter type of *Gnetum*. The gametophyte of *Peperomia*, with its sixteen free nuclei, one of which functions as an egg

nucleus, does not differ very markedly from the free nuclear type of gametophyte seen in some species of *Gnetum*. Four mitoses of the simultaneous type give rise to these sixteen nuclei, one of which becomes the egg nucleus. Between the reduction of chromosomes and the fertilization of the egg there are only four mitoses. In many angiosperms, as in *Lilium*, the interval is still shorter, the gametophyte containing only eight nuclei, resulting from three mitoses. This is the most reduced female gametophyte yet discovered in plants, and it shows only one more mitosis than does the gamete-producing generation in animals, which regularly shows two mitoses.

Up to this point I have made no mention of the tetrad of spores, a feature almost universal in plants above the thallophytes. Where the tetrad is present, the reduction of chromosomes takes place during the two mitoses by which the four spores are formed from the mother-cell. It is only in some heterosporous forms that the tetrad is incomplete or fails to appear. In such cases the reduction takes place during the first two mitoses in the mother-cells, so that whether a tetrad is formed or not, the reduction takes place during the first two mitoses in the mother-cell. To suggest that the gametophyte of the *Lilium* type represents a reduced tetrad might only cause confusion, and since the question does not affect essentially the theory proposed, I shall not discuss it at this time, but shall depend for comparison upon forms in which a tetrad is present. With a few well-known exceptions, one member of the tetrad develops, while the other three are evanescent and have no obvious function. It is only rarely that any nuclear division occurs in the three evanescent spores of the tetrad. In the functional spore of the tetrad three mitoses occur, giving rise to eight free nuclei, one of which becomes the nucleus of the egg.

I believe that this latter condition—the most prevalent one in angiosperms—corresponds closely with the egg and three polar bodies so characteristic of animals. In my opinion, the egg with its three polar bodies constitutes a generation directly comparable with the gametophytic generation in plants. The accompanying diagram (*fig. 1*) illustrates the comparison. Animals do not furnish any example more directly comparable with the condition shown in *D* of the diagram. In *D* the cell which we have compared with the

animal egg has undergone some development so that it contains eight nuclei. This is no serious objection, however, when we remember that in the pines the cell directly homologous with the larger cell in *D* contains thousands of nuclei, and in *Gnetum* contains too large

a number to be counted accurately, and within the angiosperms shows a series ranging from more than a hundred nuclei down to sixteen and then to eight. Comparatively few plants have been investigated, and it is not improbable that plants will yet be found which will complete the reduction series by showing only four nuclei, or only two, or even only one. The latter condition, with the megaspore functioning directly as the egg, would be illustrated by *C* of the diagram.

To me the comparison seems so obvious that I can explain the previous absence of a theory of alternation of generations in animals only by the fact that the gamete-bearing generation is extremely reduced and is not approached by any gradual series as in plants. Had observations in plants been confined to angiosperms, there would doubtless be no theory of alternation of generations in plants.

(2) *The male gametophyte.*—It is not necessary to trace in detail the reduction of the male gametophyte. Originally a conspicuous, independent plant, it becomes reduced, loses its independence, acquires the parasitic habit, and then undergoes a progressive reduction until it becomes a simple, microscopic, parasitic structure which no one would think of homologizing with the gametophyte of a liverwort, were it not for the close series leading to the

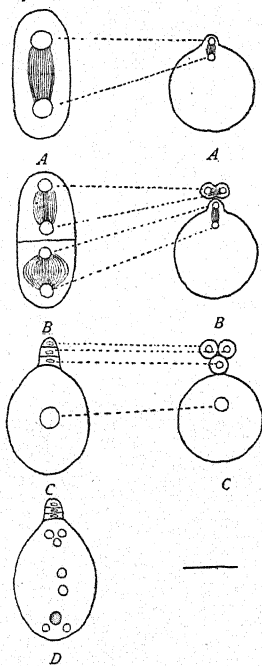


FIG. 1.—A-D, successive stages in the development of the female gametophyte in plants. The reduction of chromosomes takes place during the mitoses shown in A and B; A', formation of the first polar body; B', formation of second polar body and division of the first; C', the egg and three polar bodies; the condition shown in D is not found in animals, the gamete-bearing generation in animals having become more reduced; the shaded nucleus in D is the egg nucleus.

reduced condition. In many gymnosperms the vegetative tissue has become reduced to two evanescent "prothallial" cells, and even these are lacking in most forms. In the angiosperms it is only rarely that a vestige of the vegetative tissue in the form of a prothallial cell is found.

The formation of a tetrad of spores seems to be universal. The interval between the reduction of chromosomes and the formation of the sperm is gradually reduced, until in the angiosperms there are only four mitoses in the gametophytic generation.

I believe that the condition which prevails in angiosperms is directly comparable with that found in animals. This comparison is illustrated in the accompanying diagram (fig. 2). Here again the plant shows a slightly more extended development, the condition shown in *E* of the diagram having no parallel in animals. But, as in the case of the female gametophyte, the objection is not serious, for the male gametophyte has been gradually reduced from a conspicuous, independent plant to a microscopic, parasitic structure with only three nuclei. It is not at all improbable that instances will yet be found in which the last two mitoses have been suppressed, the microspore functioning as a sperm. This condition could then be illustrated by *E* in the diagram.

The sporogenous tissue which precedes the formation of megaspore mother-cells and microspore mother-cells is comparable with the oogonia and spermatogonia of animals. Preceding the formation of megaspore mother-cells this tissue becomes much reduced in the higher plants and in many cases is altogether lacking.

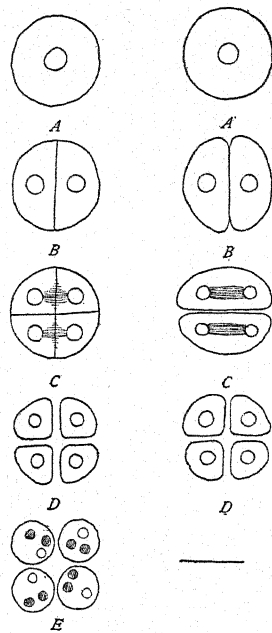


FIG. 2.—*A-E*, spermatogenesis in an angiosperm. *A*, microspore mother-cell; *B-E*, succeeding stages; the shaded nuclei in *E* represent the sperm nuclei, the unshaded nucleus being the tube nucleus; *A'*, primary spermatocyte of animals; *B'-D'*, succeeding stages; the reduction of chromosomes takes place during the mitoses giving rise to *B*, *B'* and *C*, *C'*.



2. EVIDENCE FROM THE REDUCTION OF CHROMOSOMES.—The reduction of chromosomes is a phenomenon so complex and so unique, and at the same time so essentially identical in plants and in animals, that any adequate theory must be applicable to both kingdoms. In plants the reduction always occurs during the first two divisions of the spore mother-cell, whether the plant be homosporous or heterosporous. In animals the reduction occurs during the first two divisions of the primary oocyte and primary spermatocyte. The structural character of the mitoses are too well known to need any review at this time. According to STRASBURGER<sup>2</sup> the reduction of chromosomes indicates a return to the more primitive gametophytic generation, and this view is quite generally accepted by botanists. I am aware that zoologists distinguish somatic and germ plasm, and that the application of this theory of alternation with its terms gametophyte and sporophyte (or rather similar terms, since "phyte" is obviously unsuitable) would cut the line of germ plasm, leaving part in one generation and part in the other. The sporogenous tissue of plants is quite analogous to the germ plasm of animals, and yet most botanists have no hesitation in assigning it to the sporophyte and in regarding the mother-cell as the first term of the gametophytic generation. The gametophytic generation—whether long as in the liverworts or short as in the angiosperms—is characterized by the reduced number of chromosomes; the sporophyte, except possibly in cases of parthenogenesis, contains double the number of chromosomes found in the gametophyte. We should recognize two generations in animals, characterized respectively by the reduced and the double number of chromosomes.

#### COROLLARY.

It is obvious that this theory, if well founded, affects not only the application of sexual terms in plants, but also our notions in regard to the nature of sexuality. It is hardly necessary to say that most terms relating to sexuality in plants have been borrowed from zoologists. Many botanists, especially the more rigid morphologists, have attempted to confine sexual terms to the gametophytic gener-

<sup>2</sup> STRASBURGER, E., The periodic reduction of chromosomes in living organisms. *Ann. Botany* 8:281-316. 1894.

ation, which is spoken of as the sexual generation, while the sporophyte constitutes the asexual generation. They have ceased to speak of male trees and female trees, or male flowers and female flowers, and have ceased to regard the stamens and carpels as sexual organs.<sup>3</sup>

Notions as to what constitutes a male individual or a female individual among animals, or as to what constitutes a male organ or female organ, are firmly established. If the method which the rigid botanical morphologist applies to plants should be applied to animals, the result would be interesting, for there would be no male or female individuals, nor would there be any male or female organs. All sexuality would be confined to the microscopic egg with its three polar bodies, and to the spermatocyte with its four sperms. The gametophytes of bryophytes, pteridophytes, and most gymnosperms bear well-developed archegonia, which are correctly designated sex organs, but by a gradual reduction the archegonium in the angiosperms becomes reduced to its essential structure, the egg. It is only through respect to its ancestry that this egg may be termed an organ. The antheridium is only less reduced. In animals there remain only these essential elements, which by similar courtesy may be called organs.

I prefer to apply the terminology as it is applied by zoologists, and consequently should regard dioecious sporophytes as male and female individuals. In the gametophytic generation the dioecious condition is universal in heterosporous plants. Stamens and carpels, which contain the male and female gametophytes, may be termed male and female organs as properly as may the reproductive organs of animals. It is strictly correct to speak of male and female gametophytes in plants; but in my opinion to designate the sporophyte as an asexual generation is a mistake. The sporophyte is male or female as truly as is the gametophyte; and, like the individual in animals, it is characterized by male or female reproductive organs which produce the male or female gametophytes.

I do not claim any acquaintance with zoological literature further than a reading of the latest edition of WILSON'S "The cell in development and inheritance." Were there any theories as to alternation

<sup>3</sup> Since any discussion of monoecism and hermaphroditism would neither reinforce nor weaken the argument these subjects are omitted altogether.

of generations in animals, doubtless they would have been thoroughly discussed in that book.

It is hardly necessary to state that the theory has no bearing whatever upon relationships or interrelationships. It merely adds another to the already long list of parallel processes, and suggests that the theory of alternation of generations in plants is applicable to animals.

THE UNIVERSITY OF CHICAGO.

## BRIEFER ARTICLES.

### NEW PRECISION-APPLIANCES FOR USE IN PLANT PHYSIOLOGY. II.<sup>1</sup>

(WITH FOUR FIGURES)

IN the first of these articles I gave the reasons which have led to the development of some new pieces of apparatus for educational use in plant physiology, and I described two of these pieces. In brief, believing that improvised apparatus has been brought to its fullest practicable, if not to an actually harmful, degree of development, I am trying to devise for each of the leading physiological topics appropriate normal apparatus, viz., appliances which, manufactured expressly for the specific work, will yield accurate quantitative results, will be applicable to their work with economy of time and effort, and will be obtainable by purchase at any time from the stock of a supply company. In the foregoing article I described the new clinostat and the new portable clamp-stand; below are accounts of three additional appliances, and similar descriptions of other pieces in advanced preparation will follow later. They all are now, or soon will be, for sale by the Bausch & Lomb Optical Company, of Rochester, N. Y.

#### III. AUTOGRAPHIC TRANSPIROMETER.

A practicable and obtainable form of autographic (self-registering) transpirometer, suitable for use both in educational demonstration and also in certain lines of investigation, is one of the first desiderata of plant physiology. Several forms have been devised, of which the best known are the "évaporomètre" of Richard Frères, and the registering balances of Woods and of Anderson. The first of these, while obtainable, has serious limitations both in practice and in principle; while the two others, though admirable in their accuracy, must be made to order at large cost and with much delay, and they are somewhat elaborate withal. My new instrument, illustrated in the accompanying *fig. 1*, is constructed as follows: A cylinder, shown in the upper part of the figure, contains on a spiral track between its outer and an inner wall some 250 spherical gram weights. These weights are steel bicycle balls of one-fourth inch diameter, the same as Anderson used in his balance; they weigh almost exactly one gram each,

<sup>1</sup> Continued from 37:307. April 1904.

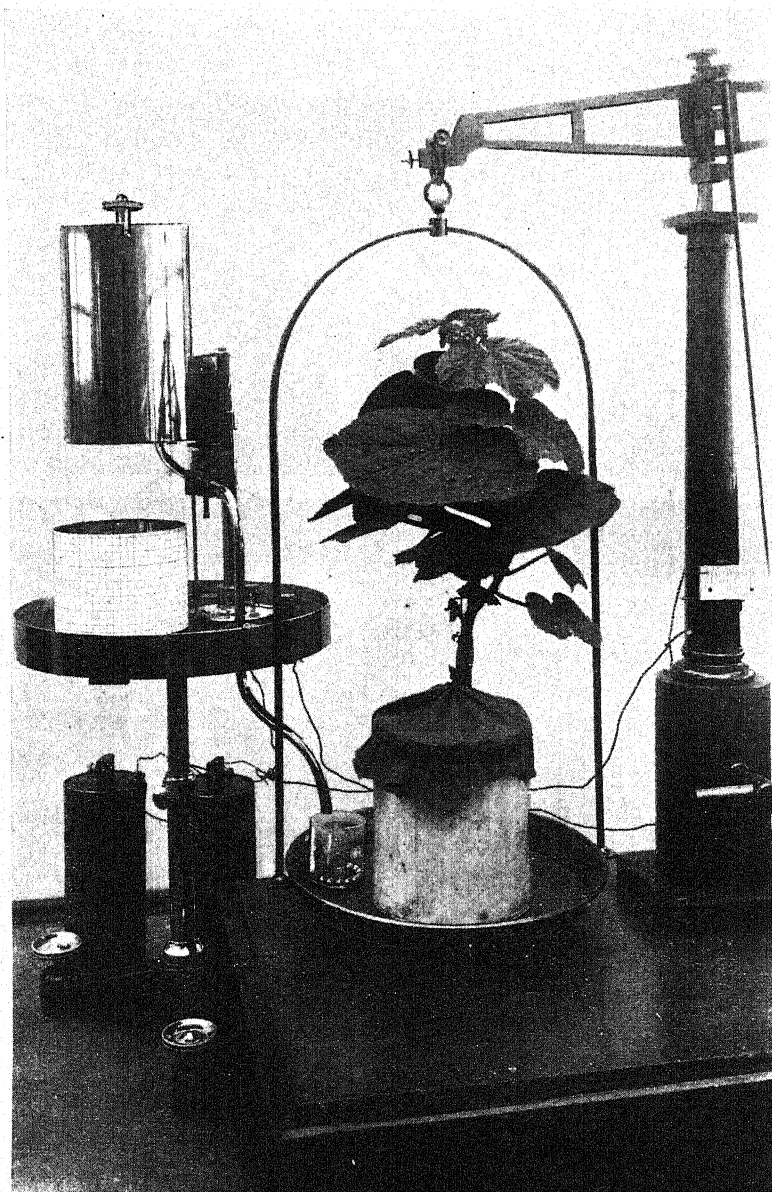


FIG. 1.

and vary not over one-thousandth of this weight from one another. These feed by gravity, one at a time, into a simple releasing valve, so arranged that when acted on by an electro-magnet a slide rises and allows one ball to drop through a tube into a scale pan, a new ball immediately taking its place in the releaser-slide. Attached to the releaser-slide is a bar carrying a pen, so adjusted that every time the slide moves, that is, every time a ball is dropped, the pen makes a vertical fine line with chronographic ink upon a record paper attached to a revolving drum. In use the plant to be studied is prepared in the manner usual for transpiration studies, and is balanced on a scale pan of any good balance, while the transpirometer is adjusted beside it. As the plant loses water this pan rises, and at the

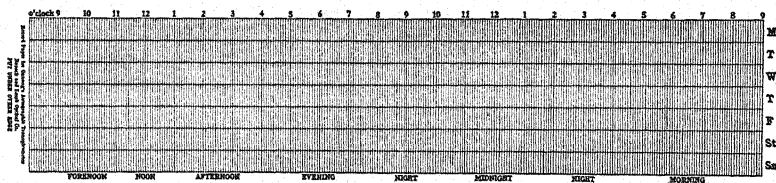


FIG. 2.—One-third the true size.

top of its swing is made to touch a wire, thus closing an electric circuit; this excites the electro-magnet, which then raises the releaser-slide, dropping a ball into the scale pan (which is immediately depressed, breaking the circuit), and making a mark on the record paper. This operation is repeated thereafter every time the plant has lost a gram of water. The drum revolves once in twenty-four hours, and the record paper, a reduced copy of which is presented in the accompanying *fig. 2*, is divided into numbered spaces corresponding to the hours; these spaces are subdivided into twelve parts, each therefore representing five minutes,<sup>2</sup> and these in turn can easily be read by estimation to fifths, or one-minute intervals. It is possible, therefore, to read off from the drum directly the number of minutes it takes the plant to lose one gram of water, data which are readily transformable into other terms. The record paper is divided into seven horizontal spaces, marked by initial letters, one for each day of the week. The pen slides on the bar, which contains seven notches; and each day, when the plant is watered and the clockwork is wound, the pen is slipped along the bar one notch. Each record paper therefore contains a complete

<sup>2</sup> These five-minute spaces are exactly 1 mm broad; hence millimeter cross-section paper may be used instead of the record paper. This happened to be the case at the time the photograph (*fig. 1*) was made.

record for a week. The tripod stand is adjustable for height, and can be leveled, while the mechanism in use is protected by a glass bell-jar.

Such is the instrument in its present form.<sup>3</sup> For some special purposes, such as for use out of doors, it would be better to have the weight-cylinder and the recording drum separated, so that the latter may be removed to any desired place in laboratory, lecture-room, or elsewhere. Probably this form will later be obtainable. For greenhouse and general demonstration use, however, the arrangement figured will be found most convenient. The releaser and reservoir are arranged for gram weights, which are the only ones likely to be needed in educational work. For special investigation purposes lighter or heavier balls could of course be used after appropriate alterations in the size of reservoir and releaser. The instrument may be used with any balance sensitive to a gram; but a special balance, adapted expressly for transpiration work, and provided with a mechanism to prevent oscillation under action of the wind, is in preparation, and will later be described.

#### IV. ADJUSTABLE LEAF-CLASP.

In several phases of the study of the physiology of leaves it is necessary to apply some object or special device to two exactly corresponding areas of the two surfaces of a leaf. The most familiar instance of this occurs in the application of Stahl's cobalt chloride method to the study of transpiration, and there are other cases nearly as important. For these purposes some simple devices are improvised from clamps, watch-crystals, mica, etc., but there is at present no obtainable appliance by which this end can be accomplished with certainty, celerity, and convenience. The new leaf-clasp, designed to meet this need, is illustrated in the accompanying *fig. 3*, and is constructed as follows. Two similar brass rings, "chamber-rings," each 30<sup>mm</sup> in diameter and 5<sup>mm</sup> in depth, are attached at the ends of parallel flexible-elastic bars, so arranged that they hold the rings firmly and exactly edge to edge, while allowing of their separation, by means of a screw, to any desired extent.<sup>4</sup> For each ring there are provided two accessory rings. One of these is right-angled in section and holds a removable cover-glass, so that when pushed over the exposed edge of the chamber-ring, it converts the latter into a glass-topped chamber, as shown in the figure. If disks of filter paper treated with cobalt chloride (and

<sup>3</sup> While this description is in press it has been decided, in order to give the instrument greater compactness, to place the weight-cylinder and recording drum side by side, instead of one above the other.

<sup>4</sup> In the final form of the instrument, a second screw, not shown in the figure, has been added, permitting the rings to be brought still more tightly together if needful.

preferably cut slightly larger than the chamber-rings so they will cling half-way up the latter) be placed in the chambers, which are then applied to the leaf, the change of color in transpiration may be observed with the greatest clearness and facility. Incidentally, the tightness of the chambers (when not on the leaf) permits the papers to retain their dryness and red color for a considerable time, so that there is no need of haste in applying them to the plant. The second accessory ring is broken, and is intended to hold tinfoil or any fabric tightly to the chamber-ring. Thus if projecting

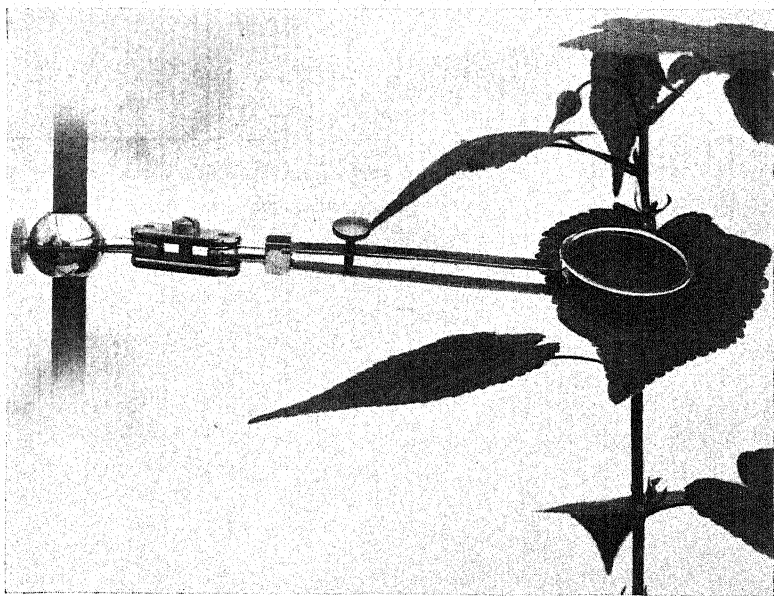


FIG. 3.

veins prevent a connection of chamber with leaf sufficiently tight for some special purposes, a band of thin rubber may be held by the broken ring in such a way that it will project against the leaf, filling the spaces between the veins. But there is a more important use for the broken ring, which is to attach tinfoil patterns or screens to the chamber-rings for the demonstration of the necessity of light in photosynthesis. The common method of demonstrating this important physiological fact by use of corks or other material attached to both faces of a leaf is fallacious (since the absence of starch thus shown is due as much to absence of carbon dioxide as to absence of light), and a logical proof involves use of



a method which cuts off light without cutting off the carbon dioxide. Most leaves have all, or most, of their stomata on the under surface, so that if this is left free, the upper surface may be covered by screens as closely as desired. By means of the broken ring a tinfoil screen, with a pattern cut therein, (preferably backed by a thin glass), or a photographic film or similar device may be attached to the inner edge of one chamber; this is then applied to the upper face of a leaf, with the lower chamber-ring pressing the leaf firmly against it. The access of light is now shut off from the lower surface by a simple accessory diaphragm arrangement (not shown in the figure), which does not impede gas passage; and such an arrangement gives a perfectly logical, and beautifully clear and conclusive demonstration of the necessity of light for starch formation. Of course, this end may be attained by simpler make-shift devices; the virtue of this instrument consists simply in the facility and certainty with which the end may be reached. As shown by the figure, a universal joint and a screw-joint fitting over any upright support permit the apparatus to be adjusted at any desired height, plane, or angle.

#### V. LEAF-AREA CUTTER.

The most striking and conclusive way of demonstrating the fundamentally important fact of increase of organic substance through photosynthesis is by SACHS'S method of comparing the morning and evening dry weights of equal areas of similar green tissue; but it is rarely employed because of the inconvenience of the manipulation. The leaf-area cutter here figured (*fig. 4*), and described below, is designed to permit all parts of this valuable experiment to be performed with exactness and facility. The cutter works on the principle of a punch; the steel dies, operated by proper handles, cut disks cleanly from a leaf between them, the disks then dropping into a perforated aluminum cup screwed below the lower die. The diameter of the punch-dies is as nearly as possible  $1.128\text{cm}^2$ , and hence every disk is nearly  $1\text{cm}^2$  in area. In use the arms of the punch are slipped above and below the leaf, when the disks may be cut very conveniently and rapidly, in any desired number, care being taken to avoid the larger veins. The larger the number taken the better, since local variations in thickness, etc., may thus be compensated, and 100 is a fair number. The cup is then unscrewed and covered by its own screw cap, which projects sufficiently to allow the cup to hang near the top of an ordinary test tube, as shown in the figure. Water in the bottom of the test tube is then boiled in the gas flame (a convenient holder for the test tube being shown in the figure), and the steam enters the perforations of

the cup, killing the living cells of the disks, thus preventing any loss of weight by respiration. The cup with its contents is then placed in the drying oven. In the evening, using the other cup, an equal number of disks is cut from corresponding positions in similar leaves, or, better, is cut from the second halves of leaves, from the first halves of which the morn-

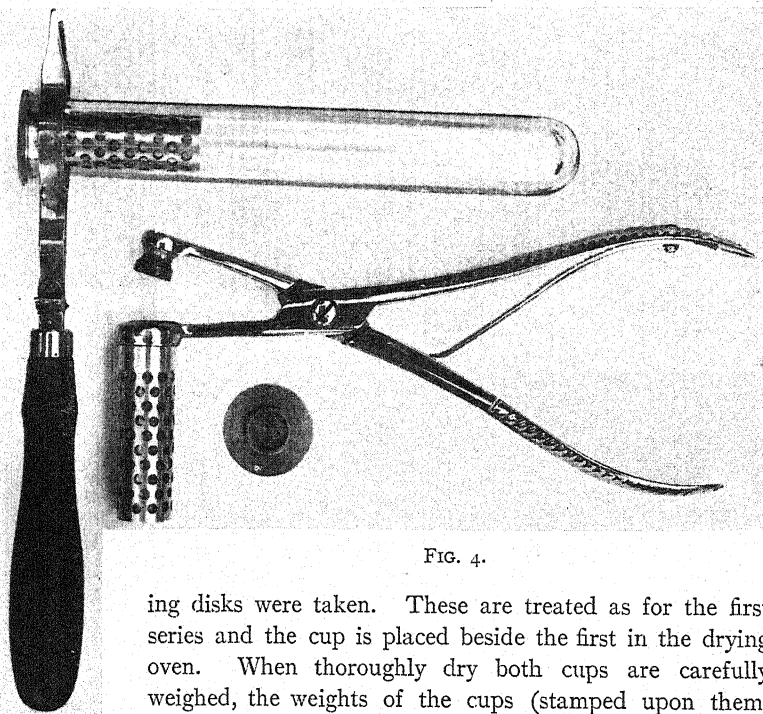


FIG. 4.

ing disks were taken. These are treated as for the first series and the cup is placed beside the first in the drying oven. When thoroughly dry both cups are carefully weighed, the weights of the cups (stamped upon them, together with the letters *M* and *N* respectively to distinguish the morning and night cups) are subtracted, when the remainder gives the dry weight, which is always greater for the evening than for the morning set. If steps be taken (by use of the methods described by SACHS) to eliminate transfer of material into the stem, the difference in the weights shows approximately the amount of substance formed through photosynthesis in the particular plant studied in so many hours per so many square centimeters of surface. In practice the performance of the instrument is very satisfactory.

In addition to the above-mentioned educational demonstration use, the instrument should also serve in those phases of ecological investigation where it is desirable to determine the relative photosynthetic powers of

various sun and shade plants, or of the same plants under sun and shade conditions. It should also permit of the determination of the photosynthetic constants of many ecologically important plants, as a part of their physiological life-histories, without a knowledge of which their real relations to their physical environment and to other competing plants cannot be understood.—W. F. GANONG, *Northampton, Mass.*

## CURRENT LITERATURE.

### BOOK REVIEWS.

#### *The teaching of biology.*

THE SIXTH volume of the American Teachers' Series is devoted to a discussion of the teaching of biology, by F. E. LLOYD and M. A. BIGELOW of the Teachers College, Columbia University.<sup>o</sup> The book is in reality two books in one cover, the first by Professor LLOYD, devoted to the teaching of botany, and the second, by Professor BIGELOW, to the teaching of zoölogy. With the latter we are not here concerned.

Dr. LLOYD considers two general topics which lie somewhat outside of his title, namely, the value of science (particularly of biology) in education, and nature study. The remaining chapters treat of the value of botany, the principles which should determine the content of the botanical course, the various types of botanical courses that have been proposed, and the botanical principles to be emphasized. These topics are followed by detailed discussion of a course in botany for high schools, and of the equipment and materials for the laboratory. The final chapter consists of a list of books most useful for teachers.

It is hardly necessary to say that such a book as this, from the hand of a successful teacher and a skilled botanist like Dr. LLOYD, will be of great service to teachers, especially to those whose training is somewhat inadequate and who therefore are familiar neither with the literature of the subject nor with those general principles and outlines which ought to be presented in secondary schools. The number of such teachers is still unfortunately large. Nor is it to be doubted that even the more experienced teachers and those better trained will profit by many of the suggestions and discussions, for Dr. LLOYD has clear, definite conceptions, and a pedagogical rather than an academic point of view. His chapter on nature study is commended to the serious attention of those who are advocates of this sort of work in the primary schools. The chapter on the "method of thought" in teaching as against the "method of discovery" is admirable in many particulars; but it must not be forgotten that even this method depends on the skilful teacher, and such an one may even "introduce a system of lenses between the eye and the object" without confusing his pupils.

The part of the book for which the author naturally expects the most criticism is that which discusses the types of botanical courses and marks out one which appeals most strongly to himself. There is no gainsaying the value of this course, and no one more strenuously than the author would insist that there are other

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<sup>o</sup> LLOYD, F. E., and BIGELOW, M. A., *The teaching of biology in the secondary school.* 12mo, pp. viii + 491. New York: Longmans, Green & Co. 1904.

courses equally valuable. It cannot be too often repeated that only the incompetent slavishly follow courses prescribed by other teachers. Each really good teacher is obliged to make his own in details, though he may follow another's general plan.

The book certainly does not overshoot its audience. One who is familiar with the teaching of botany in schools of the upper Mississippi valley and westward is tempted to think that Professor LLOYD's ideal has already been realized and perhaps even surpassed in a considerable number of the better high schools; and he wonders whether the book is not better adapted to the teachers and schools of the North Atlantic states, which, in the teaching of science, have certainly lagged behind the less conservative western ones.

It would be of no service to attempt to summarize the author's discussions, which will well repay serious consideration, and should be read both by the college man and the secondary teacher.—C. R. B.

#### A monograph on transpiration.

THE ABSOLUTE necessity that the investigator be thoroughly cognizant of what others have done and thought in his field, together with the ever-increasing hopelessness of coping with this task, offer probably the most serious discouragement to the scientific man. This difficulty, however, can be very much lessened by the publication from time to time of exhaustive monographs in restricted fields. A number of such monographs have of late years been appearing in plant physiology, the last to come to hand being BURGERSTEIN's excellent summary of the whole subject of transpiration,<sup>2</sup> a subject whose literature has been extraordinarily difficult to compass. The book is a natural growth from the author's three previous bibliographical and critical papers on this subject, *Materialien zu einer Monographie betreffend die Erscheinungen der Transpiration der Pflanzen*, which appeared from 1887 to 1901, but it is much more than a bringing of these up to date; it is not a mere critical bibliography but a thorough treatise on the various phases of the subject. New experimental data are scattered through the work, being presented in connection with the discussion of the several questions involved. Besides true transpiration, we have also discussed here the allied phenomenon, guttation, in a chapter which is altogether the best treatment that this subject has yet received. A very complete bibliography occupies thirty-three pages at the end of the volume, a bibliography in which reviews are uniformly noted as well as the articles themselves.

The subject-matter is divided logically into thirty chapters, each of which deals with a certain part of the general field. The headings of some of these are as follows: Methods of investigation, Light in general, Light rays of certain refrangibility, Atmospheric carbon dioxide, Air temperature, Humidity, Air movements, Chemicals, Periodicity, Guttation, etc. The language is clear and concise

<sup>2</sup> BURGERSTEIN, ALFRED, *Die Transpiration der Pflanzen*. Imp. 8vo. pp. x+283, figs. 24. Jena: Gustav Fischer. 1904. M 7.50.

and the matter so well arranged that the reader has little trouble in finding the discussion of any particular point in which he may be interested. Different readers will doubtless differ as to the relative importance of the several subjects, but it seems on the whole that the balance is well preserved. All workers in plant physiology will find the work practically indispensable. The only source of regret is that so many minor typographical errors should have escaped the proof reader.—B. E. LIVINGSTON.

### NOTES FOR STUDENTS.

AMONG THE MOST important ecological investigations of late years are those that have been carried on in New Zealand by COCKAYNE, which have recently brought him the degree of Ph.D., *causa honoris*, from the University of Munich. His most recent publication is an ecological presentation of the flora of the famous "southern islands."<sup>3</sup> COCKAYNE had the privileges of a government steamer, and was able to visit Auckland, Campbell, Antipodes, and Bounty Islands. Although it was necessary to make his studies with "feverish haste," his was the first ecological trip ever made to these islands, and the first botanical trip in winter. These islands lie between lat.  $47^{\circ} 43'$  and  $54^{\circ} 44' S.$ , yet in spite of the high latitude, the larger islands are clothed with a luxuriant rain-forest. Auckland Island ( $50^{\circ} 45'$ ) rarely has snow for over three days at a time on the lowlands. Although the rainfall is not excessive, almost every day is rainy or at least cloudy and the evaporation is slight. These features, together with the mild winters, make an ideal rain-forest (hygrophytic) climate. However the winds are constant and violent, a feature which commonly accompanies a xerophytic climate. The resultant vegetation reflects the peculiar climate to a most extraordinary degree. The forest trees are short (not exceeding five meters in height), and present the gnarled aspect so familiar in mountain regions and near the sea. The lateral branches grow to such length as to make the forest a true jungle. Within the forest, where the air and the forest floor are always moist, the wind does not enter; hence the vegetation is amazingly luxuriant, reminding one of the tropical forests; mosses, liverworts, and filmy ferns grow in wild profusion, making a soft carpet, while the trunks of the trees are covered with epiphytes. Even a tree fern (*Hemitelia*) was discovered, extending by some degrees the record for this ecological type. On Auckland Island there is found a typical hygrophytic forest, though with a xerophytic physiognomy such as just described; Campbell Island has merely a scrub; while Macquarie Island is without either forest or scrub. All of these islands have essentially similar climates, but the smaller islands are too exposed for trees, having instead the tussock formation. The dominant tree of these hygrophytic rata forests is the myrtaceous *Metrosideros lucida*. The much more local forests, in which *Olearia Lyallii* dominates, have a somewhat different aspect. An interesting formation, found also in the Falk-

<sup>3</sup> COCKAYNE, L., A botanical excursion during midwinter to the southern islands of New Zealand. Trans. N. Z. Inst. 36:225-333. 1904.

land Islands and Fuegia, is known as the tussock meadow; the physiognomy here is chiefly determined by grasses or sedges, which grow on mounds of their own formation, such as are sometimes seen in low sedgy pastures in North America. The tussock formation is scanty on Auckland Island, more extensive on Campbell Island, and almost excludes other formations on the smaller islands. It seems therefore that the forest and tussock form a beautiful instance of vicarious formations. Among the character tussock plants are *Danthonia bromoides* and a species of *Poa*, the former especially in subalpine tussocks. On Antipodes Island, where the wind is very severe, the tussock often grades off into a xerophytic heath-like formation, where the grasses are less dominant, being replaced by stunted *Coprosma* bushes, lycopods, and lichens. Some space is devoted to a discussion of the destructive influence of animals, which is especially marked in the sheep pastures of Campbell Island. COCKAYNE is a firm believer in the presence of a former land connection between New Zealand and these islands, because it is impossible otherwise to account for the presence of entire New Zealand formations. Certain species might be transported hundreds of miles, but scarcely the constituents of an entire formation.

In an earlier paper,<sup>4</sup> COCKAYNE has given an admirable picture of the vegetation of Chatham Island, 450 miles to the east of New Zealand. The climate resembles that of the southern islands, but is of course much milder. As would be expected, the climatic formation of the island is the hygrophytic forest, which presents a somewhat xerophytic physiognomy, though much less so than on Auckland Island. The trees commonly come close to the sea. Palms are frequent, and tree ferns are among the dominant elements, especially species of *Dicksonia* and *Cyathea*. Perhaps the dominant tree is the celastrineous *Corynocarpus*. COCKAYNE made a genetic study of the dune and bog floras. On the beach the dominant plant was once the handsome *Myosotidium nobile*, the only endemic genus of the island, now almost extinct in its native state. The dunes, once established, have been artificially disturbed, and hence show various phases of movement. In the virgin state the dunes were even forested with *Olearia* and *Myrsine*. A careful study was made of the dynamics of the bog floras, and one may find many striking parallels between these antipodean bogs and those of the United States. *Sphagnum* plays a dominant part in the early stages, but of much greater interest is the fact that the succeeding shrub stages are dominated, just as here, by shrubs of the most pronounced xerophytic structure; of course these shrubs have little or no floristic relationship with those of our bogs. Among the chief character shrubs are the ericaceous *Dracophyllum*, the restionaceous *Leptocarpus*, and the rubiaceous *Coprosma*. *Carex* is also conspicuous in the early stages. The first tree is the composite, *Olearia*. Then comes the typical forest, as described above. On the table land, *Senecio Huntii* (also an arborescent composite) and *Dracophyllum arboreum* dominate the early forest stage. Many

<sup>4</sup> COCKAYNE, L., A short account of the plant-covering of Chatham Island. Trans. N. Z. Inst. 34:243-325. 1902.

of the characteristic bog plants are just as characteristic of dry as of wet xerophytic situations; this is true of *Olearia*, and notably so of *Phormium tenax*, the New Zealand flax. This plant, once so abundant, is being exterminated by fires and grazing animals, and is now almost confined to the seemingly opposite habitats rocks and lake margins. Fires have wrought great destruction to the native flora and as a result there are vast areas dominated by the typical fireweed, *Pteris esculenta*; the exotic *Rubus fruticosus* also covers large areas.

DENDY<sup>5</sup> has also written concerning the flora of Chatham Island. He thinks that the absence of many characteristic New Zealand types is due to the absence of many typical New Zealand habitats, such as alpine and other xerophytic situations, as well as to the long time that has elapsed since the islands were connected with New Zealand; even when there was a land connection, it is likely that much of it was a desert, and hence a barrier to many forms.

An earlier paper by COCKAYNE<sup>6</sup> deals with the vegetation of the New Zealand mainland, in the neighborhood of the Waimakariri River. In this paper there are brought out the characteristic features of the eastern and western climatic regions, and their various edaphic formations.—H. C. COWLES.

THE PREMATURE decease of NICOLAS ALBOFF has been much mourned by plant geographers. His studies in Fuegia have been edited and issued by EUGÈNE AUTRAN,<sup>7</sup> who has published as a preface an appreciative biographical sketch, together with a bibliography and an excellent portrait. In the historical summary, especial praise is given to the work of HOOKER more than half a century ago. There are two dominant formations, the forest and the moor. The forests are extremely dense and luxuriant, and bear witness to the humidity and uniformity of the climate. The forest floor has a wealth of bryophytes and filmy ferns. Extreme floristic poverty characterizes these forests, only two tree species being present: *Fagus antarctica* and *F. betuloides*. Moors occur where the forest cannot exist, either through exposure or soil moisture. Kerguelen Island, 140° distant, represents, from a floristic standpoint, the farthest point reached by this Fuegian flora. The balsam bogs or dry moors, so characteristic of the Falkland Islands, are also found in Fuegia. Fifty-three per cent. of the species are endemic. The most interesting elements in the flora are the neozelandian and boreal. ALBOFF agrees with most authors in holding to an ancient antarctic continent or archipelago, as accounting for the similar floras throughout antarctic regions. The long-known and most perplexingly large boreal element has been a stumbling

<sup>5</sup> DENDY, A., The Chatham Islands; a study in biology. Manchester Memoirs 46: 1-29. 1902. See Bot. Cent. 89: 728-729. 1902.

<sup>6</sup> COCKAYNE, L., A sketch of the plant geography of the Waimakariri River Basin, considered chiefly from an oecological point of view. Trans. N. Z. Inst. 32: 95-136. 1900.

<sup>7</sup> ALBOFF, NICOLAS, Essai de flore raisonnée de la Terre de Feu. Anales del Museo de La Plata. Sección Botánica. I. pp. vi+85+xxiii. With portrait. La Plata. 1902.



block to students of floristics. Apart from species that are more or less cosmopolitan, the author holds that alternating glacial climates, advocated by CROLL, afford the best explanation for the similarity of austral and boreal floras. Since glacialists generally reject CROLL's hypothesis, it is seen how slender a support ALBOFF's theory has. To the reviewer, it seems that here, if anywhere, we shall be forced to consider, at least as a possibility, BRIQUET's polytopic (polygenetic) theory.

In connection with the work of ALBOFF, brief mention may be made of DUSÉN's admirable studies in the same region. DUSÉN's earlier work has been noted in these pages.<sup>8</sup> One of his papers<sup>9</sup> was for the most part a floristic and taxonomic account of the flora. A later paper<sup>10</sup> presented a more detailed ecological account of the vegetation, along the line of the short earlier articles. His latest paper<sup>11</sup> gives an excellent account of the ecological and floristic features of western Patagonia. There are three great regions: the evergreen forest, the deciduous forest, and the steppe. The evergreen forest resembles that described by ALBOFF, and for New Zealand by COCKAYNE. Bryophytes, especially liverworts, form a forest floor, sometimes five or six feet thick. Epiphytes reach a high degree of development. One or more species of beech everywhere dominate, although *Drimys Winteri* and *Libocedrus tetragona* are often abundant, the latter especially in moory soil. Of extraordinary interest is the deciduous forest, the only one yet found in the southern temperate zone. The dominant tree is *Fagus (Nothofagus) antarctica*, the very tree that dominates so much of the evergreen forest. Very few cases are known, at least on the lowlands, where one tree species dominates in two radically different climatic forest types. The whole forest aspect differs, being more parklike, and without the luxuriant undergrowth of the evergreen forests. The rich bryophyte carpet of the latter is wholly missing. The steppes call for no special mention. Through the work of ALBOFF and DUSÉN, it is clearly to be seen that the Fuegian and Patagonian vegetation is of almost equal interest to the ecologist as the vegetation of New Zealand.—H. C. COWLES.

ITEMS OF TAXONOMIC INTEREST are as follows: J. RICK (Ann. Mycologici 2:407. 1904) has described *Pseudohydnum* as a new genus of fleshy fungi from South America.—A new part of KOMAROV's *Flora Manshuriae* (Acta Hort.

<sup>8</sup> See BOT. GAZ. 24:135. 1897. Also Engl. Bot. Jahrb. 24:179-196. 1898.

<sup>9</sup> DUSÉN, P., Die Gefässpflanzen der Magellansländer, nebst einem Beitrage zur Flora der Ostküste von Patagonien. Svenska Expeditionen till Magellansländerna. 1900. See Bot. Cent. 85:47-49. 1901.

<sup>10</sup> DUSÉN, P., Die Pflanzenvereine der Magellansländer, nebst einem Beitrag zur Oekologie der magellanischen Vegetation. Svenska Expeditionen till Magellansländerna 3:351-523. 1903. See Bot. Cent. 96:468-469. 1904. Also Engl. Bot. Jahrb. 33:litt.28-29. 1903.

<sup>11</sup> DUSÉN, P., The vegetation of western Patagonia. Reports of the Princeton University Expeditions to Patagonia, 1896-1899. Part I. Princeton. 1903.

Petrop. 22:453-787. *pls.* 1-17. 1904) begins with Rosaceae and ends with Balsaminaceae, bringing the serial numbers of species to 1058.—P. A. RYDBERG (Bull. Torr. Bot. Club 31:555-575. 1904), in his 12th paper entitled "Studies on the Rocky mountain flora," has described new species of *Draba*, *Smelowskia*, *Sophia* (2), *Arabis* (2), *Erysimum* (2), *Opulaster* (2), *Holodiscus*, *Potentilla*, *Rosa* (2), *Astragalus* (2), *Homalobus* (3), *Ceanothus*, *Sphaeralcea* (2), *Touterea* (2), *Acrolasia* (2), *Epilobium* (4), *Gayophytum*, *Anogra* (2), *Pachylophus* (2), *Gaura*, *Suida*, *Aletes*, *Phellopterus*, and *Pseudocymopterus*.—H. A. GLEASON (Ohio Nat. 5:214. 1904) has published a new *Helianthus* from Illinois.—H. REHM (Hedwigia 44:1-13. *pl.* 1. 1904) has published *Trichophyma* (Myriangiales) and *Stictoclypeolum* (Mollisiaceae) as new South American genera of fungi from the Ule collection.—H. CHRIST (Bull. Herb. Boiss. II. 4:10 9-1104. 1904) has described new species of Costa Rican ferns under *Asplenium* (2), *Lomaria* (3), *Adiantum* (3), *Gymnogramme* (2), *Saccoloma*, and *Polypodium* (3).—G. HIERONYMUS (Bot. Jahrb. 34:417-560. 1904) has published Lehmann's pteridophytes from Guatemala, Colombia, and Ecuador, enumerating 315 numbers, and describing new species in *Trichomanes* (2), *Hymenophyllum* (2), *Loxsomopsis*, *Cyathea*, *Nephrodium* (6), *Aspidium*, *Polystichum*, *Diplazium* (2), *Blechnum*, *Gymnogramme* (5), *Adiantum*, *Polypodium* (12), and *Elaphoglossum* (7).—E. L. GREENE (Leaflets 1:65-81. 1904) has described 5 new species of *Ceanothus*; has separated from *Gentiana* the genus *Pneumonanthe*, to include the "closed gentians" and their allies, and has transferred to it nearly 30 species; and has described from middle California new species under *Lupinus* (4), *Lotus*, *Sidalcea* (2), *Silene*, *Aquilegia*, *Delphinium*, *Bistorta*, *Eriogonum*, *Swertia*, *Castilleja* (2), *Pentstemon*, *Apocynum*, *Cryptanthe*, *Galium*, and *Chrysothamnus* (2).—R. M. HARPER (Torreya 4:161-164. 1904) has recognized a new species of *Ludwigia* (*L. maritima*) among the forms commonly referred to *L. virgata*.—C. F. MILLSPAUGH (*idem* 172) has published a new species of *Euphorbia* from the Bahamas.—W. H. BLANCHARD (*Rhodora* 6:223-225. 1904) has described a new *Rubus* (blackberry) from New England.—H. D. HOUSE (*idem*. 226 *pl.* 59.) has described a new *Viola* from New England.—J. M. C.

WIELAND<sup>12</sup> has secured transverse seed-sections of one of the Bennettitales showing tissue filling the archegonium, which he interprets as the proembryo. If he is correct, this is an interesting confirmation of the current morphological view that the Ginkgo type of proembryo is the most primitive among living gymnosperms. The previously known mature seeds of Bennettitales are singular among gymnosperms in the entire absence of endosperm; and now even in this reported proembryonic stage WIELAND finds no trace of endosperm.—J. M. C.

<sup>12</sup> WIELAND, G. R., The proembryo of the Bennettiteae. Am. Jour. Sci. IV. 18:445-447. *pl.* 20. 1904.

## NEWS.

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DR. OSCAR BREFELD, professor of botany at Breslau, has retired from active service.

DR. JOHANN GOROSCHANKIN, professor of botany in the Imperial University and director of the Botanical Gardens at Moscow, died recently at the age of sixty years.

PROFESSOR GEORGE J. PEIRCE has returned from working at the Zoölogical Station at Naples and resumed his duties at Leland Stanford University at the beginning of the year.

THE FORESTRY QUARTERLY, whose chief editor is Professor B. E. FERNOW, has increased its subscription price to \$2, as the amount of material for publication demands an issue of three to four hundred pages a year.

HENRI T. A. HUS, M.S., a graduate of the University of California and a student with HUGO DE VRIES, has been appointed to take charge of the herbarium work at the Missouri Botanic Gardens, St. Louis. Mr. HUS has given much attention to fasciation and to mutations in plants.

NOTICE.—Owing to the increasing pressure upon our space, and in justice to numerous contributors, the Editors of the BOTANICAL GAZETTE are constrained to announce that with the beginning of volume XL (July 1905) no paper exceeding thirty pages in length (about 11,000 words) can be accepted for publication, unless the author is willing to pay for additional pages; in which case the size of the number will be correspondingly increased. Longer papers that have already been received and accepted will be published in due time.

Attention is also directed to the more liberal terms for separates announced in the advertising pages.

ON JANUARY 12 Captain JOHN DONNELL SMITH, of Baltimore, presented his private herbarium and botanical library to the Smithsonian Institution. The herbarium consists of more than 100,000 mounted sheets of vascular plants, besides many specimens of the lower cryptogams; and the library contains nearly 1,600 volumes substantially and elegantly bound. This is by far the most important botanical gift ever received by the Institution, and it is a valuable addition to the rapidly accumulating collections that are making Washington a great center for taxonomic work. Captain SMITH will retain for the present the custody of his library and the greater part of his collection, but some 25,000 specimens have already been sent to Washington.

## BOTANICAL GAZETTE

MARCH, 1905

GAMETOPHYTES AND EMBRYO OF TORREYA TAXIFOLIA.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY.  
LXIX.

JOHN M. COULTER and W. J. G. LAND.

(WITH PLATES A, I, II, III)

*Torreya taxifolia* Arnott<sup>1</sup> occurs in a narrow belt along the eastern side of the Apalachicola River, extending from the southern boundary of Georgia for about thirty miles southward (1). In April 1904 this region was visited by H. C. COWLES of this laboratory, among whose notes the following are of interest in this connection:

My visit was to the northernmost colony, west of Chattahoochee village, and close to the Georgia line. The distribution lines on CHAPMAN's map (1) would lead one to suppose that the tree is xerophytic and frequents the steep and dry eastern bluffs. I was much surprised to find that it was confined (in the Chattahoochee station at least) to the extremely mesophytic slopes of ravines, growing exclusively in the shade of trees, and in places that are continually moist, preferably on slopes facing north. The northern and southern known limits of the tree are only about thirty miles apart, and the east-west range is much less. Furthermore, on account of the great economic value of the wood, and the familiarity of the tree to all the inhabitants of the region, the likelihood of finding other areas is very slight.

It is associated with a remarkable and somewhat extensive group of northern mesophytic plants, and the conclusion is irresistible that *Torreya* is a northern plant of the most pronounced mesophytic tendencies, and to be associated with

<sup>1</sup> Unfortunately, *Torreya* was used at least three times as a generic name, in as many families, before 1838, the date of the publication of *Torreya* Arnott. Hence ARNOTT's genus has been replaced by *Tumion* Raf., and our species becomes *Tumion taxifolia* Greene. In the present paper, however, the more familiar name is used for convenience.

such forms as the beech-maple-hemlock forms of our northern woods, our most mesophytic type of association. Probably it never becomes a large tree, although farmers always cut the trees as soon as they become at all usable. Rarely were any found over 30<sup>cm</sup> in diameter or more than 9 to 12<sup>m</sup> high. It has remarkable capacity for vegetative reproduction, almost equaling the redwood in this respect. Many suckers issue from cut stumps, and even from fallen trunks; even rotten stumps show vigorous suckers, and it seems to be as tenacious of life as the poplar. Staminate trees appear to be the more numerous; however, when in blossom they are far more conspicuous than are the pistillate trees, and the conclusion as to proportion may not hold.

COWLES secured collections of staminate and ovulate material April 4 and 5, and arranged for subsequent collections to be sent to the laboratory. These collections were made at intervals of approximately two weeks up to October 21. The strobilus-bearing twigs were packed in damp cotton in tightly closed tin buckets and reached the laboratory in good condition in about five days. The length of the intervals between collections and between collecting and killing has prevented so close a series as is desirable at certain stages, but the gymnosperm periods are so long that a fair outline of morphological events was secured.

#### SPERMATOGENESIS.

STROBILI.—The staminate strobili occur in the axils of leaves of young shoots. Their appearance in October, on a shoot of the same season, is shown in *fig. 1*. At this time they are small and ovoid, solitary in the axil of each leaf, and by a curving of the short peduncles are displayed along the under surface of the shoot. The strobilus consists of a series of closely overlapping sterile bracts, in four vertical rows, completely enveloping the tip of the axis bearing numerous stamens. It is thus distinctly sterile below and fertile above, the sporophylls continuing the spiral succession developed by the bracts (*figs. 6 and 7*).

The young strobili were first observed in July, and at that time no primordia of sporophylls were evident; but in August these were beginning to appear. *Fig. 7* is from a longitudinal section through a strobilus at this period (August 12), showing the overlapping sterile bracts and the beginning of staminal primordia. A remarkable development of the pith region of the axis below the staminate por-

tion of the strobilus, with its investing vascular cylinder, may be observed, apparently an important storage region for the strobilus.

STAMENS.—At the stage of the staminal primordia observed August 12, there is no evident differentiation of tissues (*fig. 8*), but early in September the young sporangia become distinct, the sporogenous tissue being represented in each case by a single primary sporogenous cell. At this stage the further development of the young sporangia differs. Seven sporangia are seen in the primary sporogenous cell stage, three adaxial and four abaxial (*fig. 10*), radially arranged about the central axis as are the five or more sporangia in the allied *Taxus*. The four abaxial sporangia develop in the usual way, and become the pendent abaxial sporangia characteristic of *Torreya*. The three adaxial sporangia, however, do not develop further, the primary sporogenous cell not dividing, and its nucleus showing signs of disorganization (*fig. 9*). The disorganization continues until it involves all the cells separating the three adaxial sporangia, which are thus replaced by a single large flattened cavity, which becomes a resin cavity. Intermediate stages were found in which the three sporogenous regions were still distinct (*fig. 10*). In *fig. 11* (October 21) is shown a median longitudinal section through a stamen, in which the large resin cavity is seen above and the normally developing sporogenous tissue below. As a result, the mature stamen of *Torreya* is characterized by four abaxial sporangia and a large adaxial resin cavity.

In one instance the two lateral sporangia were smaller than the middle ones (*fig. 10*), suggesting a tendency to still greater reduction in the number of sporangia. Accordingly *Pinus Laricio* was examined, and two resin cavities were found related to the two sporangia exactly as the two lateral sporangia of *Torreya* are to the middle ones; and in early stages the tissue on the sites of these two resin cavities of *Pinus* resembles that of sporangia. It is interesting to note that in *T. californica* Miss ROBERTSON (8) found occasional stamens bearing six or seven mature sporangia, indicating that in these cases some or all of the usually abortive sporangia reached maturity.

There is evident a tendency to reduce the number of functioning sporangia by abortion, a reduction that has proceeded farther in *Pinus* than in *Torreya*; and in the latter farther than in *Taxus*. That

the cavities formed by the breaking down of young sporogenous and adjacent tissue should become resin cavities in conifers is to be expected.

It was only in the abortive sporangia of *Torreya* that stages were found indicating the history of the sporangium up to the primary sporogenous cell stage. For example, from *fig. 9* it seems evident that there was a single hypodermal archesporial cell, which at this stage had given rise to two layers of wall cells and a single primary sporogenous cell. In the mature sporangium there are three or four wall layers. The epidermis contains numerous stomata, and its cells become prominent and have thickened walls. The sporangia are bluntly four-angled from pressure, and the epidermal cells at the angles are much larger than elsewhere.

MALE GAMETOPHYTE.—We secured no stages between the very young sporangium and the shedding of the pollen, which occurs late in March and early in April. Miss ROBERTSON (8) has observed the mother-cell stage and the formation of tetrads in *T. californica*.

In germination the microspore of *T. taxifolia* cuts off no prothallial cell, a feature common to all the Coniferales except Podocarpeae and Abietaeae. After the first division the generative and tube cells are distinct and separated by a very delicate wall or membrane. The tube nucleus is sometimes spherical, but more often amoeboid (*fig. 12*).

Early in April the binucleate pollen grains, rich in starch, were found resting on the nucellus (*fig. 19*); and at the end of June micropyles were found full of pollen grains, most of which had sent out no tubes, but were still full of starch, nucleate, and apparently alive.

As fertilization occurs about the middle of August, active pollen tubes occupy the sterile cap of the nucellus about four months, and their behavior is exceedingly variable. They may advance towards the embryo sac rapidly, reaching it at a very early stage, as early as June 21, when the endosperm consists of only sixteen to sixty-four parietally placed free nuclei (*figs. 14* and *15*); or they may advance slowly, being found at all stages of progress at the same date. They may advance so directly that the tube resembles a straight cleft through the nucellar tissue to the sac, or they may pursue a remarkably devious course. In one case a tube passed directly half-way

down the nucellar cap, then advanced spirally downward and outward until it reached the peripheral cells of the nucellus, and after destroying several of these it turned abruptly inward, penetrated the nucellus at the level of the archegonium, crossed the top of the endosperm, and discharged its contents into the archegonium on the farther side. In another instance, such a pollen tube had entered the inner integument and destroyed some of its cells before turning back into the nucellus. It is very common for the pollen tube to push into the sac at its free nuclear stage, making a deep invagination, often to the middle; from this pocket the tube turns back again into the nucellus. It is of interest to note in this connection that the usually solitary archegonium is never centrally placed in the endosperm, and the pollen tube enters the sac to one side of it (*fig. 16*).

In all the wanderings of the pollen tube, the body cell, stalk nucleus, and tube nucleus are conspicuous. The division of the generative cell was not observed, but that it occurs very early in the development of the tube is evident. The body cell is relatively very large, with a conspicuous nucleus and investing cytoplasm, and was always found consorting closely with the stalk and tube nuclei (*figs. 13 and 14*).

The division of the body cell just before fertilization results in unequal male cells (*fig. 23*), almost exactly resembling those of *Taxus*. It is not a case of the extrusion of one nucleus from the common cytoplasm, as observed by COKER (2) in *Podocarpus*, but the cytoplasm is unequally divided, so that there are two distinct and naked male cells very different in size. The whole cavity of the pollen tube surrounding the cells and nuclei is rich in starch and other food materials (*fig. 13*).

A consideration of the time involved in these various events shows that a period of about fifteen months elapses between the first appearance of the microsporangiate strobilus and fertilization, divided as follows: June, first appearance of strobilus; August, first appearance of staminal primordia; September, distinct differentiation of sporangia; April, shedding of spores; August, fertilization. The strobilus was first observed in July, but in such a condition that it must have been evident in June, if not earlier. In comparing this schedule with that given by Miss ROBERTSON (8) for *T. californica*, it is evident



that the sporangium in both species passes the winter in the mother-cell stage, but that the subsequent stages appear earlier in *T. taxifolia* growing in its natural habitat than in *T. californica* growing in England. For example, in the latter case the reduction division takes place about the time that *T. taxifolia* sheds its pollen, and pollination in *T. californica* does not seem to occur until late in May or early in June.

#### OÖGENESIS.

**STROBILI.**—The ovulate strobili are borne in the axils of the lower leaves of short young shoots (*fig. 2*). They usually occur in pairs upon a very short axillary branch, usually one pair, frequently two pairs, very rarely three pairs appearing upon a single shoot. A cluster of two to six strobili, therefore, appears near the base of the strobilus-bearing shoot, the upper pairs never maturing, usually one and sometimes both strobili of the lowest pair producing the large plum-like seeds (*fig. 3*). The strobilus is a very simple one, consisting of four enveloping bracts and a single terminal ovule with two integuments (*figs. 17* and *18*), the outer one often called an arillus because it ripens fleshy. The whole structure resembles a simple ovulate flower with a perianth of four bracts, which perhaps deserve to be called a perianth as much as the so-called perianth of Gnetales; but it is none the less evident that they are the sterile bracts of a much reduced strobilus.

The strobili were first seen July 26, at which time the growing point, enclosed by the bracts, was composed of entirely homogeneous tissue, showing no differentiation as an ovule (*fig. 17*). No subsequent stages were found until April 7 (*fig. 18*), when the mother-cells were in synapsis (*fig. 20*); and it seems probable that the winter was passed in the mother-cell stage. At this time the integuments are entirely free from the nucellus, appearing to arise from the base of the ovule. Soon, however, extensive intercalary growth below the mother-cell becomes evident, the ovule being greatly elongated and broadened below, the original free nucellus with its integuments forming only the tip. This growth continues throughout the season of fertilization and the following one; and OLIVER (6), who has described this intercalary growth in *T. nucijera*, estimates that in that species in the maturing seed the original nucellus with its free

integuments represents only one-twentieth of the entire length of the seed. The characteristic structures of the integuments are continued as two distinct peripheral layers of this large mass of additional tissue, and the tissue within these layers may be taken to represent in a similar way the downward extension of the nucellus. It is this additional nucellar tissue that the endosperm chiefly invades, giving rise to the phenomenon of "rumination," to be described later. OLIVER (7) has also described fully the course of the vascular strands in the ovule of certain species of *Torreya*, a description which seems to serve as well for *T. taxifolia*.

**FEMALE GAMETOPHYTE.**—The mother-cell is solitary and with no differentiation of a nutritive mechanism about it, such as appears in connection with the "spongy tissue" of *Pinus*, and in all the *Pinaceae* investigated. In *Torreya* it is directly in contact with the cells that are resorbed, without any intervening digestive layer (*fig. 20*). Since this is true also of *Podocarpus* (2) and *Taxus* (10), it suggests the possibility that *Taxaceae* in general may be characterized by the absence of a special digestive layer about the mother-cell.

The reduction division was not seen, but a more or less complete tetrad is formed, as observed by Miss ROBERTSON (8) also in *T. californica*.

The germination of the megaspore begins with the usual free nuclear division, the nuclei being in the parietal position when only sixteen to thirty-two in number (*figs. 14 and 15*). The interior of the sac contains cytoplasmic material, much less dense than the cytoplasm of the parietal layer, and also some reserve food. In this early few-nucleate stage of the endosperm there is always an appearance suggesting that the sac has sent a beak-like projection, containing a nucleus, upwards into the nucellar tissue (*fig. 15*). After a careful comparison of the position of this apparent projection in reference to the surrounding parts with that of the megaspore, it seems that the "projection" is the original site of the megaspore, and that the appearance of a projection is due to the fact that the sac has encroached almost exclusively upon the chalazal tissue. This conspicuous beak, containing one of the parietal nuclei, often appears close to the tip of an advancing pollen tube, and suggests a possible explanation of the peculiar behavior ascribed to the archegonium

initial of Tumboa. Inasmuch as the archegonium initial of *Torreya* often occupies this beak, the suggestion becomes still more pertinent (*fig. 21*).

The formation of walls in the endosperm was not observed before July 1, and in several instances they did not appear for a month later. When wall-formation began, repeated countings showed 256 free nuclei, which seems to be a very common limit of free nuclear division among gymnosperms.

Since fertilization was observed August 12, it is evident that the archegonium is developed very early in the history of the gametophyte. In fact, as soon as the very small sac is filled with extremely delicate tissue the archegonium initial becomes evident. It does not seem possible for archegonia to appear any earlier, for the initials are organized as soon as the free nuclear stage has passed. In *Torreya*, therefore, nearly all of the endosperm, which becomes an extensive tissue, develops after fertilization.

The single archegonium initial is always to one side of the central axis (*fig. 16*), often occupying the "beak" referred to above, and so projecting above the endosperm (*fig. 21*). A neck cell is cut off and divides antichinally, forming a two-celled neck (*fig. 22*), the usual limit of neck-formation among gymnosperms. In fact, it is only among Podocarpeae and Abietae that a more extensive neck is usually formed, consisting of more than one tier of cells, unless the somewhat anomalous neck of *Ephedra* be included. The fact that there is variation in the number of neck cells in the same form (two to twenty-five in *Podocarpus*), and that as a rule necks are destroyed as soon as formed by the growth of the central cell and pollen tube (*fig. 23*), suggests that their extent depends somewhat upon the approach of the pollen tube, which usually checks neck formation early, but sometimes permits it to become more extensive. In *T. californica* Miss ROBERTSON (9) has found that the archegonia are usually three in number, ranging from two to five, and that the necks consist of four or six cells.

The central cell enlarges rapidly, no jacket-layer being evident until after fertilization, and even then it is weakly organized (*fig. 25*). The nucleus is spherical and lies near but not against the neck cells, more nearly resembling an egg nucleus than in any gymnosperm

we have observed (*fig. 22*). We could not detect the formation of a ventral canal cell or nucleus, or anything that stood for such a structure at later stages. A ventral nucleus was expected, for a distinct ventral canal cell among Coniferales seems to be restricted to the Abietae and does not always occur in them, and there seemed to be no excuse in our preparations for missing it. We are fully aware that all previous negative evidence as to the occurrence of at least a ventral nucleus in archegonium-forming gymnosperms has proved to be deceptive, but a study of the behavior of the central cell of *Torreya*, from the formation of the neck cell to fertilization, not only failed to show any indication of division but suggested that it may not occur. In *T. californica* a spindle seen twice in the central cell was interpreted by Miss ROBERTSON (9) as representing the "cutting off" of a ventral nucleus, but no other traces of it could be found.

In the single case in which two archegonia were observed, they were at opposite sides of the gametophyte, with the tip of a pollen tube between them.

At the time of fertilization the gametophyte contains 400-800 cells, with extremely thin walls and scanty cytoplasm (*fig. 23*). The only differentiation observable is the abundant accumulation of reserve food in the peripheral cells of the antipodal region. The whole mass of endosperm at this period usually measures 20 by 30 $\mu$ ; while in the mature seed the endosperm mass is ordinarily about 20<sup>mm</sup> long by 14<sup>mm</sup> at its widest part, and all of it surcharged with starch and other food materials. The food material is particularly conspicuous in a broad central band extending from the advancing tip of the embryo and widening to the antipodal end of the sac. *Fig. 5* shows the longitudinal extent of the band, and *fig. 4* its cross-section. The peculiar behavior of the endosperm after fertilization will be considered under the discussion of the maturing of the seed.

#### FERTILIZATION.

The forcible discharge of the contents of the tube may be inferred from the vacuole-like appearance in the center of the egg, produced by the inrush (*figs. 24 and 25*). The male nucleus in its cytoplasmic sheath passes through the cytoplasm of the egg and comes in contact with the egg nucleus. The male cytoplasm becomes closely appressed

to the surface of the female nucleus, slips from its own nucleus, and was observed extending over fully two-thirds of the female nucleus (fig. 24). This behavior of the male cytoplasm has been observed by COKER (3) in *Taxodium* and by Miss ROBERTSON (9) in *Torreya californica*. The male cytoplasm of *Torreya taxifolia* is sharply differentiated by staining from the cytoplasm of the egg, and undoubtedly completely invests the fusion nucleus. The appearance of a similar mass of cytoplasm investing the free nuclei of the first division (fig. 25), and continued in the second division in connection with wall-formation (fig. 26) suggests the possibility that the male cytoplasm may remain differentiated through more than one cell generation. Near the neck end of the archegonium nuclei are evident, which seem to be the stalk and tube nuclei and the other male nucleus with its investing cytoplasm (fig. 24).

#### EMBRYO.

Soon after fertilization the first division of the egg nucleus was observed (fig. 25), and almost immediately the second division follows, giving rise to four large free nuclei almost filling the egg (fig. 26), one nucleus in the base of the egg, the other three in a plane above. At this time wall-formation occurs, the cytoplasmic radiations which precede it being very evident (fig. 26). Two weeks later the egg is completely filled with a proembryo consisting of twelve to eighteen cells (fig. 27). This complete filling of the egg by the proembryo is remarkable among Coniferales, having recently been observed also by LAWSON (4) in *Sequoia*, but as yet not recorded in other genera. In *Torreya*, at least, this fact seems to be related to the relatively small size of the egg, the very large nuclei, and the early appearance of walls.

The cells of the proembryo at this early stage are distinctly in three tiers; that nearest the neck of the archegonium comprising five or six cells and forming the primary suspensor tier; the middle tier, comprising five or six cells and forming the secondary suspensor tier; and the lowest consisting of a single cell which ultimately contributes to suspensor-formation and forms the embryo. The inequality in the number of cells entering into the tiers seems to be characteristic of Taxaceae. In *Podocarpus* COKER (2) found the three tiers made up

of eleven cells in each of the upper two and one in the lowest; and a similar but less striking inequality is to be observed in *Taxus*. Occasionally in *Torreya* other divisions may occur, giving rise to approximately four tiers and a proembryo of about eighteen cells; but no other division occurs until the following spring, the winter condition being a proembryo of three or four tiers of cells as described above.

In the following season the suspensor develops and the embryo is formed, along with the characteristic "rumination" of the endosperm and the development of the testa. The first indication of change from the winter proembryonic condition is the elongation of the primary suspensor cells (*fig. 29*); a little later this is shared by the secondary suspensor cells; and this is followed by the elongation of the third tier, if four tiers are formed. In the meantime the terminal cell has begun a series of rapid divisions, resulting in a cylindrical mass of meristematic tissue, much as LYON (5) has described in the case of the embryo of *Ginkgo*. This meristematic cylinder advances gradually into the endosperm, its basal tiers of cells successively contributing to the suspensor elongation. Thus in the formation of the suspensor there seems to be developed what may be called a wave of elongation, beginning with the uppermost tier of the proembryo and extending gradually downward, tier after tier, until it includes the upper region of the meristematic cylinder formed by the terminal cell. This same phenomenon is very evident also in *Thuja*.

After the meristematic cylinder has advanced into the endosperm and has become prominent, the growing points are organized; the two cotyledons presently becoming beautifully crescentic in outline and completely surrounding the stem-tip; and the root-tip being organized deep within the meristematic cylinder.

In several instances a number of small embryos were observed imbedded in the endosperm about the suspensor region of the normal embryo. Our material did not permit any determination of their origin, but they resemble the proembryo of the normal embryo, and are developed while the latter is in its second season's growth. After the pollen tube has reached the archegonium, the endosperm grows up around it (*figs. 23 and 24*), so that the tube lies in a cup-shaped depression. After fertilization, the rim of this endosperm cup con-

tinues growth and gradually incloses the fertilized egg, in most cases forming quite an elongated beak above the embryo. Later many of these cells round off, forming a loose tissue, and it is among these rounded-off cells that the feeble accessory embryos are produced. Whether these have been developed apogamously from the endosperm cells, or have budded from the suspensor cells can only be conjectured. In any event, they might develop further if there was any failure in the development of the normal embryo.

The time involved in the series described above, that is from the first appearance of the megasporangiate strobilus to the maturity of the seed, is about thirty months, distributed as follows: June (?), first appearance of the strobilus; April, mother-cells in synapsis; August, fertilization; October, proembryo of 12 to 18 cells (winter condition); following season, development of embryo, "rumination" of endosperm, and development of testa; October, fall of seed.

#### MATURING OF SEED.

The outer integument and its histological continuation about the ovule develops a thick fleshy coat containing very numerous large resin cavities, and completely inclosing the structures within (*figs. 4 and 5*). This fleshy coat gives to the mature seed the appearance of a plum (*fig. 3*), as in the seeds of Cycads and Ginkgo. Within the broad band of resin cavities, near the inner limit of the integument, two conspicuous vascular strands occur, directly opposite one another (*fig. 4*). These are the main strands of the very characteristic vascular system of the ovule described by OLIVER (7).

The inner integument early differentiates into two distinct layers, a differentiation just as evident in Cycads and Ginkgo. The outer layer forms the stony coat, and the transformation from soft to very hard tissue begins after the embryo and endosperm have completed their development. The hardening begins at the apex of the ovule, and on account of resistance to stains appears under low power as a clear band (black in *fig. 5*). The hardening band gradually extends downwards through the relatively very short integument, and differentiating as a distinct layer in the much larger mass of tissue below completely invests the ovule within the fleshy coat. Protoplasmic connections between the cells of the stony coat and striations in the cell walls are unusually clear.

The inner layer of the inner integument comprises several layers of thin-walled cells, but beyond the integuments it is not histologically differentiated as a layer distinct from the tissue within. Accordingly, through the great bulk of the seed this layer may be neglected, and the whole mass of tissue within the stony layer and outside of the embryo sac will be spoken of as nuclear tissue or perisperm.

The behavior of the endosperm is peculiar, resulting in what is called "ruminated endosperm," a phenomenon peculiar to *Torreya* among gymnosperms, and commonly illustrated by the nutmeg. "Rumination" of endosperm proves to be a misnomer, for the endosperm is always the successfully aggressive tissue in developing this condition. The perisperm continues to grow throughout the maturing of the seed, and the final condition results from what might be called the struggle of two growing tissues that have been abutting upon one another through their whole period of growth.

In ordinary seeds the endosperm invades the surrounding tissue more or less uniformly; in the case of Cycads and Ginkgo, for example, obliterating most of the perisperm. In *Torreya*, on the other hand, the invasion by the endosperm is irregular in the extreme. It is in the season after the proembryo has been formed that the active invasion of the perisperm begins. The extension of the endosperm into the tip of the nucellus above the sac proceeds in the usual way, obliterating all of it except a few peripheral layers of cells. This uniform invasion seems to be due to the fact that in this apical region (the original nucellus) the perisperm is not growing actively if at all. Below this small region at the tip, however, the perisperm is very active and evidently resists disintegration much more at certain points than at others. As a consequence, the perisperm becomes eroded by the irregularly advancing endosperm, and is left in the condition of a much dissected coast-line (*figs. 4 and 5*). To the casual observer this results in an appearance suggesting that the endosperm is being invaded by plates of perisperm, but this is no more true than that the promontories of a dissected coast-line are advancing into the sea. The suggestion of an invading perisperm is further strengthened by the fact that within the perisperm bordering the endosperm a dark brown and finally black band of cells is developed, due to abundant food storage (*figs. 4, 30, 31*), but this really recedes as the endosperm advances.



A cross-section of the mature seed always shows a definite and deep constriction of the endosperm in the center, exactly opposite the two opposed vascular strands that run up on each side of the seed through the inner part of the outer integument (*fig. 4*). This constriction is the cross-section of two opposite and deep longitudinal furrows in the endosperm, and it means that in this longitudinal plane the endosperm encounters the greatest resistance in invading the perisperm. This most resistant perisperm certainly seems to hold a very definite topographical relation to the principal vascular strands, and this relation may explain the resistance.

That endosperm is the aggressive tissue at every point, even at the region of most resistant perisperm, is evident for several reasons. In no case were the peripheral cells of the endosperm broken down; and in no case did there fail to appear one or two layers of disorganized cells of the perisperm in contact with the endosperm (*figs. 30* and *31*). In every case, also, the peripheral cells of the endosperm appeared active and very vigorous, and their different appearance in regions of more and less active encroachment is striking. In regions of active invasion the endosperm cells are radially elongated, and many of them are binucleate (*fig. 30*); while in regions of less active invasion the cells are more nearly isodiametric and rarely binucleate (*fig. 31*).

Another proof that endosperm is the encroaching tissue may be obtained from comparative measurements. At the times of fertilization the gametophyte usually measures 20 by 30 $\mu$ . In the mature seed the ordinary length of the gametophyte is 20<sup>mm</sup>, the greatest width being 14<sup>mm</sup>, and the least (at the deep constriction opposite the vascular strands) 1.5<sup>mm</sup>. At this most resistant region of the perisperm, therefore, where it is hard to escape the conviction that the perisperm plate has cut the endosperm nearly in two, the endosperm has increased its diameter against the perisperm seventy-five times.

The best reason, however, for concluding that the endosperm is the invading tissue in this case is that this is always the behavior of endosperm; and it is singular that the old explanation of "rumination" was ever suggested. An examination of the nutmeg, the classic illustration of "ruminated endosperm," and of *Asimina triloba*,

showed that precisely the same explanation applies to them that we have given in the case of *Torreya*.

#### SUMMARY.

The staminate strobilus consists of a series of closely overlapping sterile bracts, in four vertical rows, completely enveloping the tip of the axis bearing numerous stamens. The large adaxial resin cavity that occurs in the stamen occupies the site of three abortive sporangia.

The male gametophyte has no prothallial cell, and the male cells are very unequal, resembling those of *Taxus*. The pollen tube is exceedingly variable in the rate and direction of its advance through the nucellar cap, sometimes pushing in the embryo sac while it is in an early free-nucleate stage.

The ovulate strobilus consists of four enveloping bracts and a single terminal ovule with two integuments. Extensive intercalary growth below the mother-cell forms the bulk of the mature ovule and seed. There is no organization of a special digestive layer around the mother-cell.

The solitary archegonium initial appears as soon as walls are formed, is always at one side of the central axis of the gametophyte, and forms a two-celled neck. The nucleus of the central cell was not observed to divide, nor could any trace of a ventral nucleus be found.

In fertilization the male cytoplasm invests the fusion nucleus, and seems to remain distinct until wall-formation at the four-nucleate stage of the proembryo.

In the development of the proembryo, four free nuclei appear before wall-formation, and the proembryo completely fills the egg, having no "open cells." A proembryo of twelve to eighteen cells is the winter stage. In the spring the suspensor is formed by what may be called a wave of elongation, beginning with the uppermost tier of the proembryo, and extending gradually downward, tier after tier, until it includes the upper region of the meristematic cylinder formed by the terminal cell.

Small embryos are formed during the second season in the suspensor region of the normal embryo; but whether they arise from prothallial or suspensor cells was not determined.

The "rumination" of endosperm, peculiar to *Torreya* among gymnosperms, arises from the extremely irregular encroachment of the endosperm upon the perisperm, the endosperm being resisted much more at certain points than at others. The same was found to be true of other "ruminated" seeds.

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#### EXPLANATION OF PLATES I-IV.

With the exception of *Plate I*, all figures were drawn with the aid of an Abbé camera lucida and reduced one-half in reproduction. Abbreviations are as follows: *br*, bract; *a*, primordium of stamen; *oi*, outer integument; *ii*, inner integument; *r*, resin cavity; *n*, nucellus; *pc*, pollen chamber; *s*, sporogenous cells; *tn*, tube nucleus; *g*, primary spermatogenous cell; *sn*, nucleus of stalk cell; *b*, body cell; *m<sub>1</sub>*, functional male cell; *m<sub>2</sub>*, functionless male cell; *hr*, haustorial region of female gametophyte; *nc*, nucleus of neck cell; *o*, egg; *end*, endosperm; *per*, perisperm.

## PLATE A.

FIG. 1. Staminate branch; October 21, 1904.  $\times 1$ .

FIG. 2. Ovulate branch; April 7, 1904.  $\times 1$ .

FIG. 3. Mature seed; October 21, 1904.  $\times 1$ .

FIG. 4. Cross-section of seed showing ruminated endosperm with storage region in center, seed coats, stored food in the perisperm, and resin ducts.  $\times 3$ .

FIG. 5. Longitudinal median section through seed showing embryo, ruminated endosperm, and seed coats.  $\times 3$ .

## PLATE I.

FIG. 6. Transverse section through a staminate strobilus showing bracts and primordia of stamens; August 12, 1904.  $\times 24$ .

FIG. 7. Longitudinal section through a staminate strobilus showing enveloping bracts, primordia of stamens, and storage region; the position of the bundles is shown by the dotted lines; August 12, 1904.  $\times 24$ .

FIG. 8. Primordium of a stamen; August 12, 1904.  $\times 460$ .

FIG. 9. Median section through an adaxial sporangium showing the disorganizing primary sporogenous cell and two wall cells; October 21, 1904.  $\times 460$ .

FIG. 10. Cross-section of a sporophyll showing the three abortive adaxial and the three functional abaxial sporangia; October 21, 1904.  $\times 47$ .

FIG. 11. Longitudinal section through a stamen showing early stage of the resin cavity above and a functioning sporangium below; October 21, 1904.  $\times 255$ .

FIG. 12. Pollen grain showing primary spermatogenous cell and tube cell; April 7, 1904.  $\times 1250$ .

FIG. 13. Tip of a pollen tube which has penetrated about half way through the nucellus; June 10, 1904.  $\times 460$ .

FIG. 14. Tip of pollen tube in contact with the embryo sac; the female gametophyte is in the free nuclear stage and the nuclei are placed parietally; June 21, 1904.  $\times 460$ .

FIG. 15. Embryo sac in free nuclear stage showing one of the nuclei occupying the place of the megaspore mother-cell; June 10, 1904.  $\times 185$ .

FIG. 16. Pollen tube in contact with the endosperm; an archegonium is at the left of the tube; July 26, 1904.  $\times 255$ .

## PLATE II.

FIG. 17. Young ovulate strobilus showing enveloping bracts, inner integument, and nucellus; July 26, 1904.  $\times 47$ .

FIG. 18. Ovulate strobilus showing bracts, integuments, nucellus with rudimentary pollen chamber, and megaspore mother-cell; April 7, 1904.  $\times 24$ .

FIG. 19. Tip of nucellus with pollen chamber containing a microspore; April 8, 1904.  $\times 220$ .

FIG. 20. Megaspore mother-cell in synapsis; April 7, 1904.  $\times 460$ .

FIG. 21. Micropylar end of female gametophyte with archegonium initial projecting into the space formerly occupied by the megaspore mother-cell; July 26, 1904.  $\times 460$ .

FIG. 22. Archegonium consisting of two neck cells and central cell; the nucleus of the central cell has rounded out, and is passing downward to the center of the cell and taking on the appearance of an egg nucleus; July 26, 1904.  $\times 460$ .

FIG. 23. Median longitudinal section of female gametophyte showing egg, remains of a neck cell, and antipodal haustorial cells; the tip of the pollen tube in contact with the egg contains stalk and tube nuclei, functional and functionless male cells; the upward growth of the endosperm cells forms a sheath around the pollen tube; August 12, 1904.  $\times 460$ .

PLATE III.

FIG. 24. Fertilization; the male nucleus is in contact with the egg nucleus; the cytoplasm of the male cell is closely applied to the egg nucleus; the functionless male cell, and tube and stalk nuclei are in the upper part of the egg cytoplasm; the cavity in the egg cytoplasm is caused by the inrush of the contents of the pollen tube; August 12, 1904.  $\times 460$ .

FIG. 25. Two-celled proembryo; the dense cytoplasmic mass surrounding the nuclei is probably in greater part derived from the male cytoplasm; August 27, 1904.  $\times 460$ .

FIG. 26. Four-celled proembryo; walls coming in; August 12, 1904.  $\times 460$ .

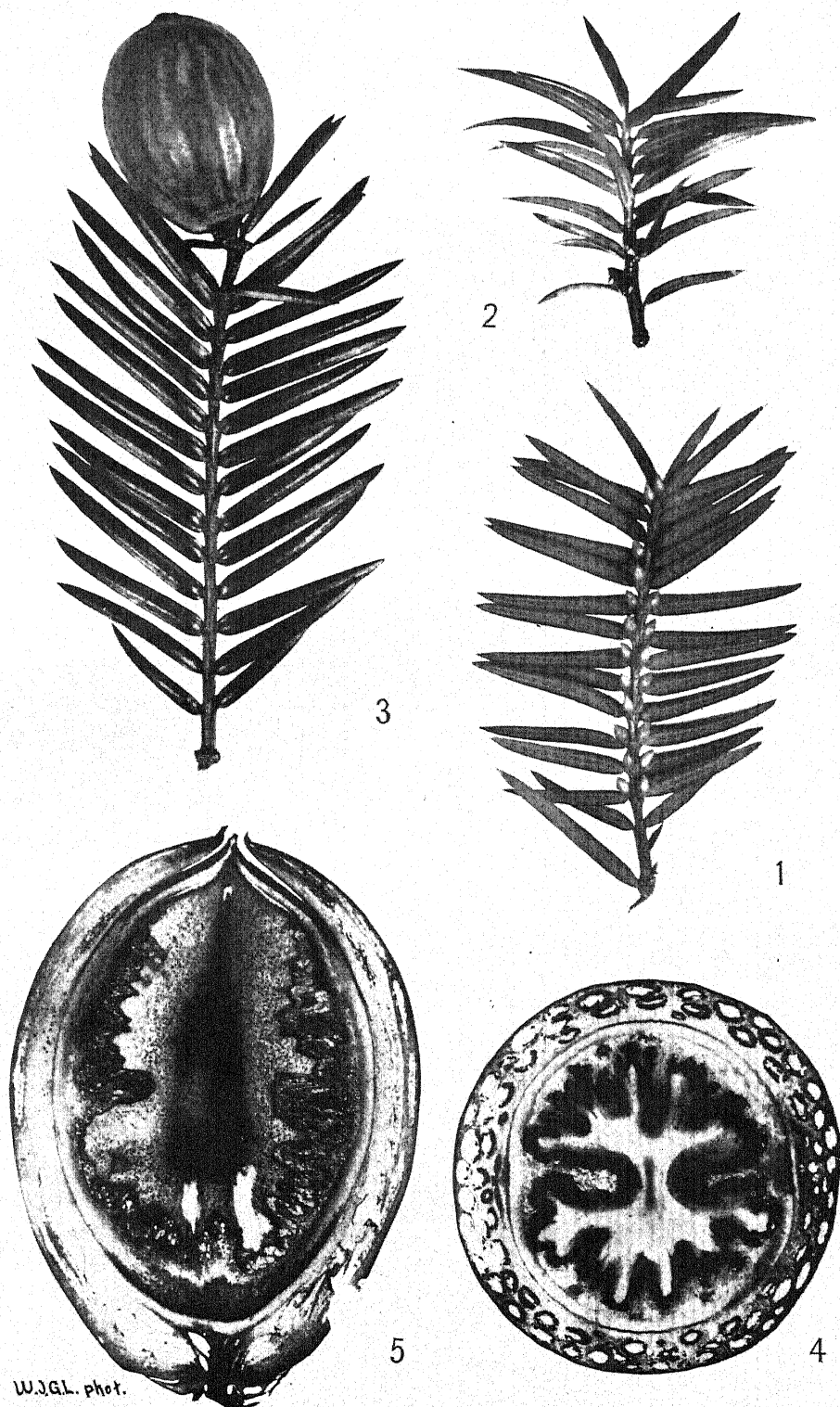
FIG. 27. Proembryo shortly after walls are laid down; the proembryo passes the winter in this stage; August 27, 1904.  $\times 460$ .

FIG. 28. Cross-section through suspensor cells; September 12, 1904.  $\times 460$ .

FIG. 29. Proembryo showing elongation of suspensor cells; April 7, 1904.  $\times 460$ .

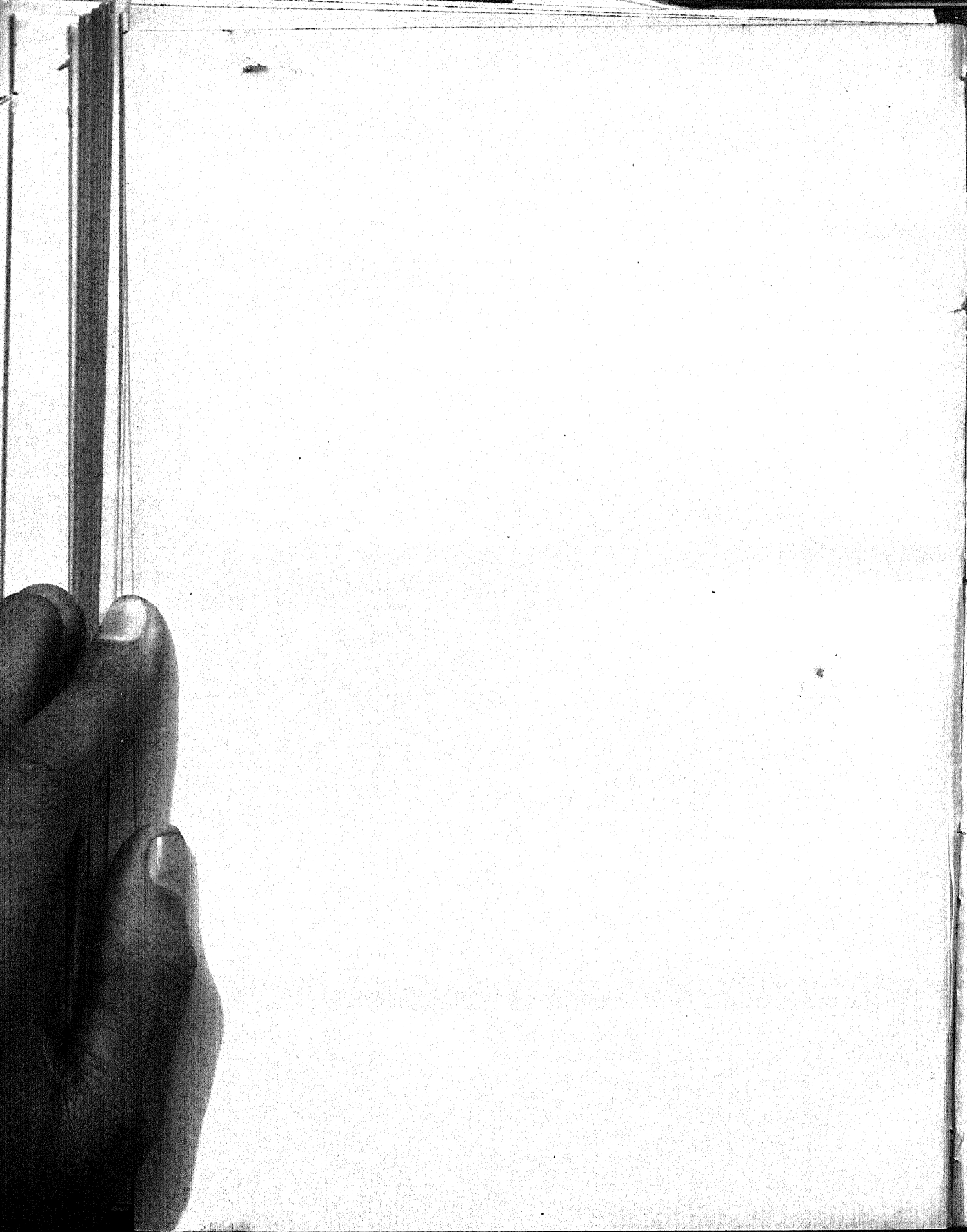
FIG. 30. Endosperm cells encroaching on perisperm; August 12, 1904.  $\times 640$ .

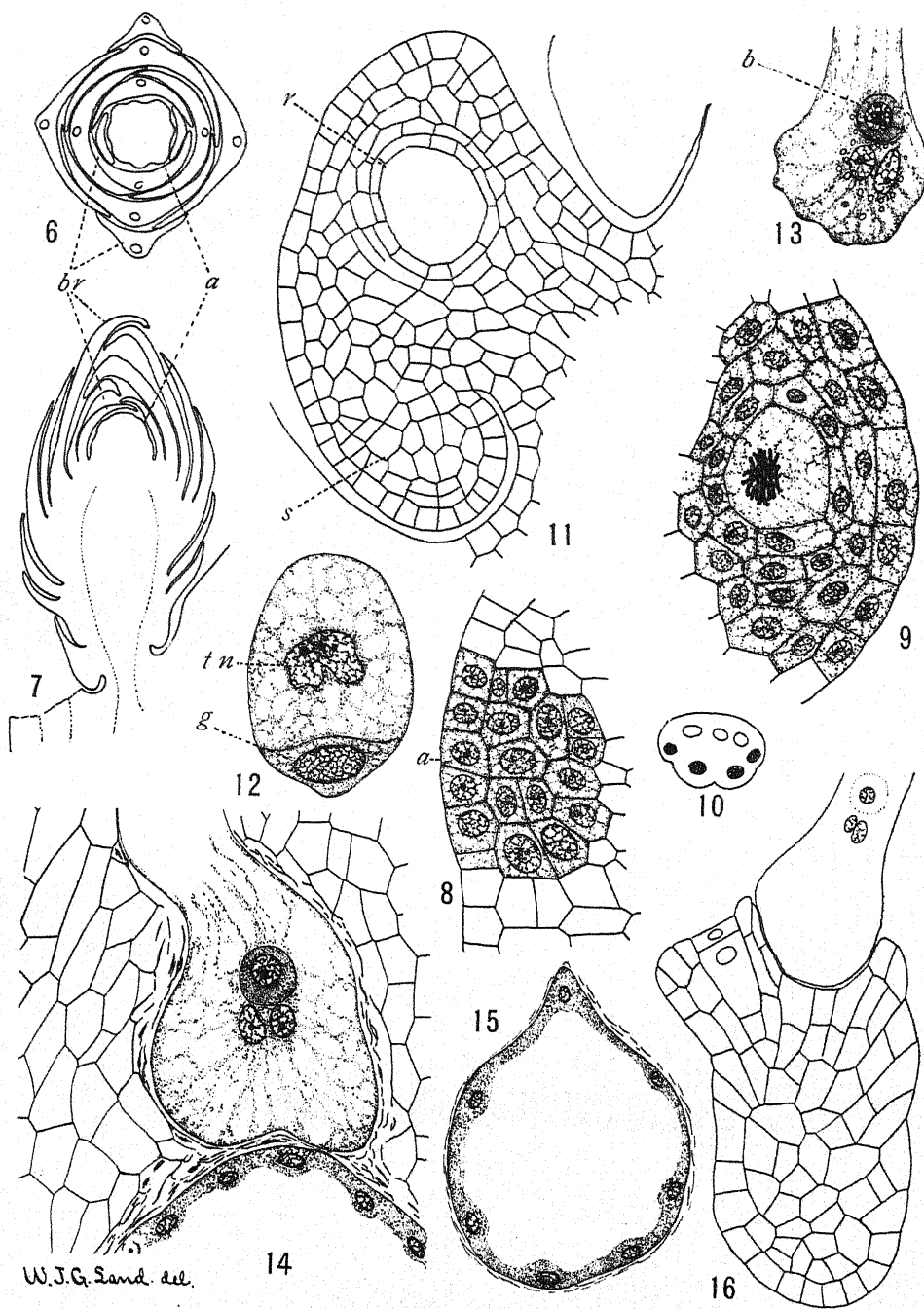
FIG. 31. Endosperm cells which have ceased to encroach on perisperm; August 12, 1904.  $\times 460$ .



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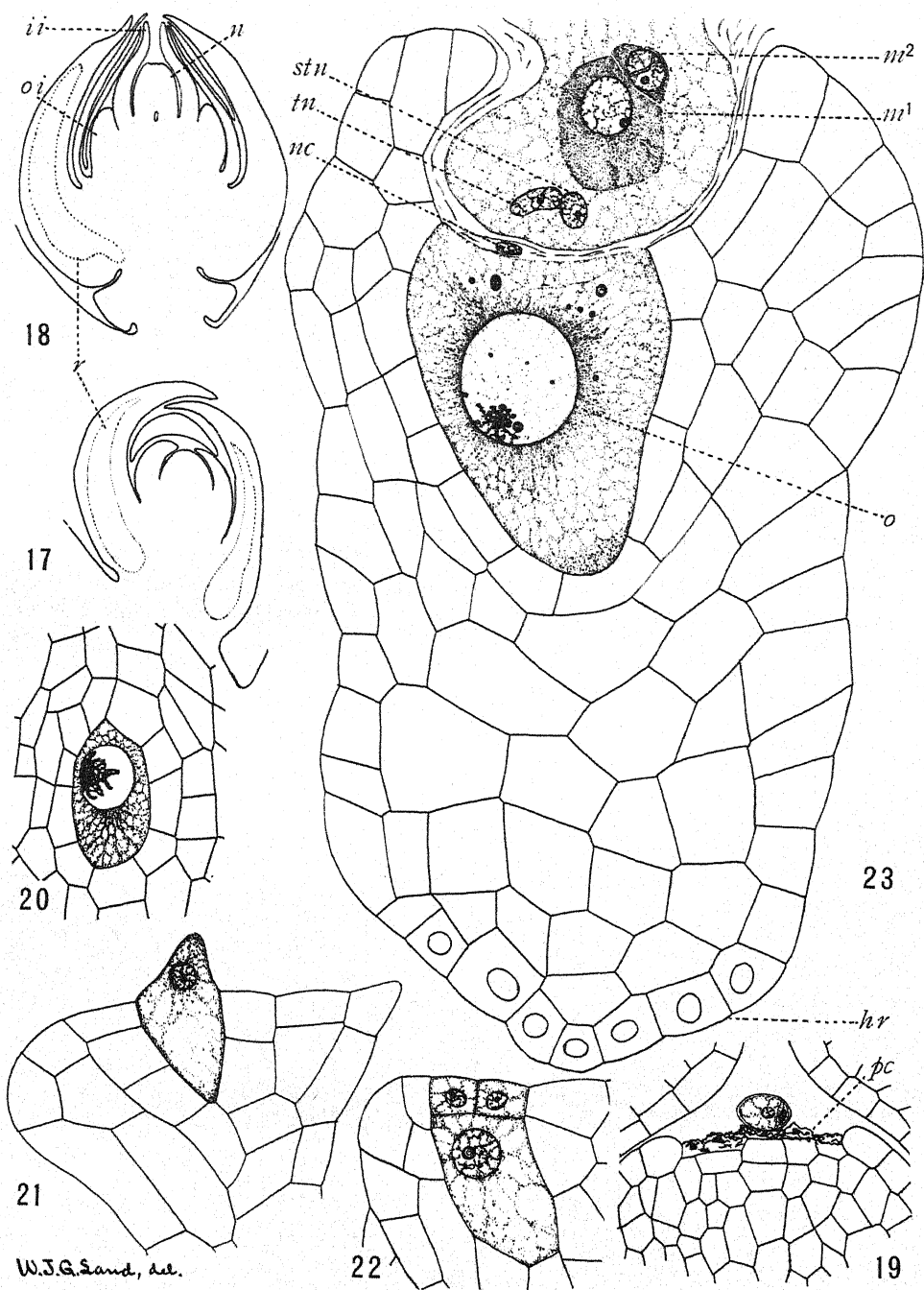




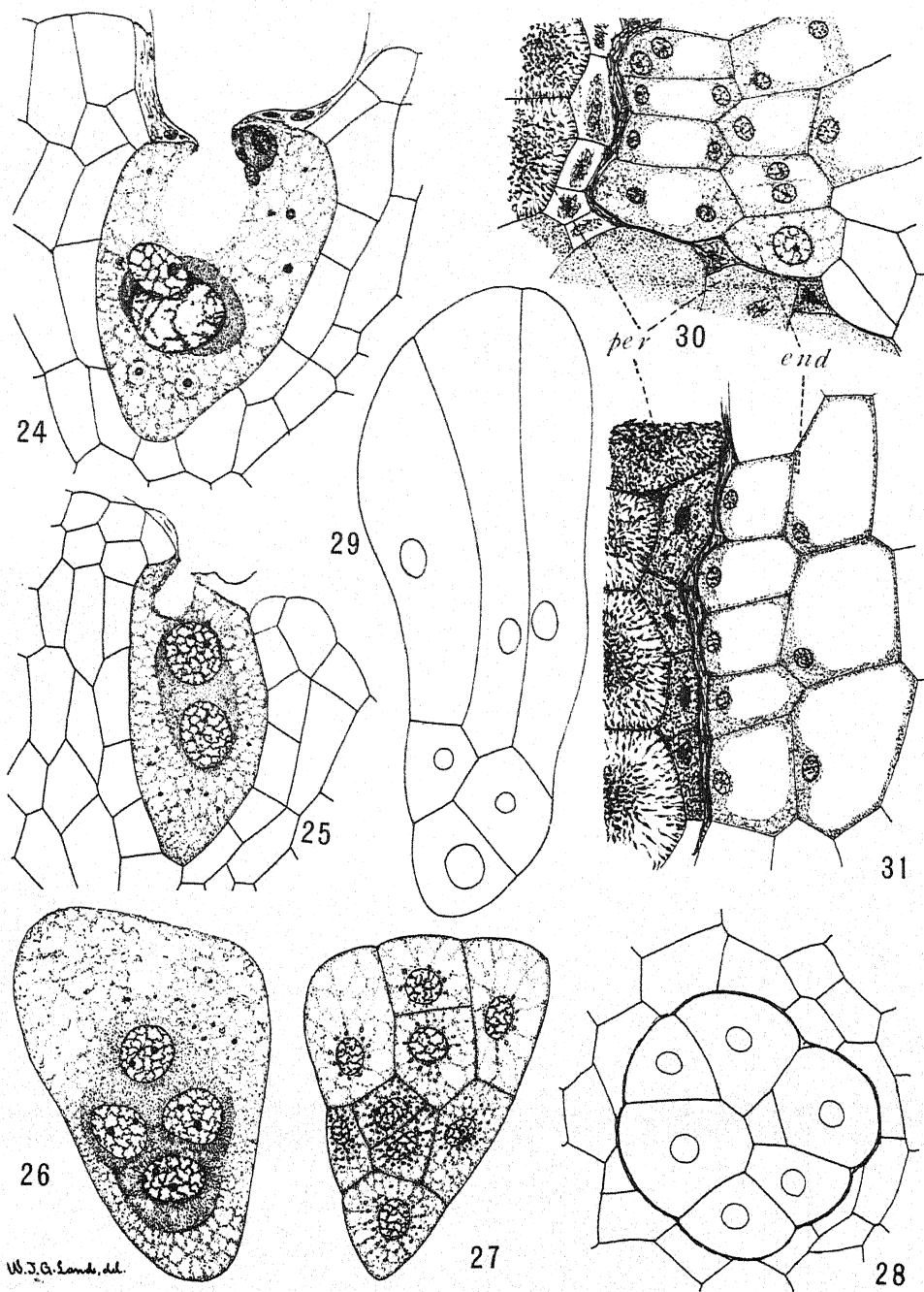














## THE PRINCIPLES OF PHYTOGEOGRAPHIC NOMENCLATURE.<sup>1</sup>

PEHR OLSSON-SEFFER.

THE confusion prevailing within the nomenclature of phytogeography has of late been repeatedly brought up for discussion. A unanimous opinion exists as to the disadvantages resulting from the present chaotic terminology. Such a diversity of ideas prevails that every writer is obliged to explain in what sense he has used a technical term, and if he omits an explanation we are often left in doubt as to the interpretation of the expression used. An agreement has to be arrived at, sooner or later, and the sooner there is an end to the present disorder, the better for the progress of phytogeography and all concerned.

This science is still in its infancy and very few of its doctrines are settled beyond doubt. We meet with contradictory views at every step. Sweeping generalizations, often based upon very imperfect observations, and described in vague and uncertain terms, full of ambiguities, threaten the development of this important science. Its advancement and success depend upon well-settled methods of investigation and description. The necessity of adopting a nomenclature similar to that of other descriptive sciences is obvious. The prevalent fault of which we complain is not the absence of names and technical terms, but of the defective definition of the terms now in use. It has always been much easier to offer censure than to correct mistakes, easier to state evils than to relieve them. My object in this paper is not to give any proposals as to the detailed arrangement of phytogeographical nomenclature, but to discuss some of the general principles which ought to prevail in any attempt to revise the nomenclature so as to meet the present demands of the science. I have elsewhere, in papers appearing simultaneously with this, drawn attention to the terminology of certain phytogeographical phenomena.

<sup>1</sup> Read before Section G of the American Association for the Advancement of Science, Philadelphia meeting, December 30, 1904.

Since the appearance of the papers of WARBURG, FLAHAULT, NILSSON, and CLEMENTS on this vexed question of nomenclature, it could have been expected that some discussion would arise, but instead it seems as if phytogeographers were content with the opinions brought forward, although these are by no means harmonious. The object of plant geography is the study of the distribution of plants, and of the laws that govern this distribution, not wrestling with words nor philological hair-splitting. But it cannot be denied, as I have just said, and as is generally conceded, that this science needs uniformity of expression; how to obtain this is the problem.

The next international congress, to be assembled at Vienna in June 1905, is to take this matter under consideration. Some of the foremost phytogeographers of the world constitute a committee which is to make a report and submit certain proposals that may or may not lead to a solution of the problem. It is only the general principles, however, that can be laid down by any one botanist or any joint committee, because it is quite beyond the power of any one except the individual monographer to decide what expression may be necessary in his individual case. But so long as each one is allowed to do what he thinks is right, there will be no end of the present trouble. What we need is a good, clear system of wholesome general rules. The practical and gradual application of these must be left to the discrimination of the individual writers, who have to describe conditions essentially different in different cases. The reader is then the judge whether the writer has succeeded in his application of the rules, whether his terminology is correct or not. No permanent international committee is needed for the purpose of acting as a guardian or a court. If a good code of rules for nomenclature is laid down, it will be followed spontaneously by all writers of any consequence, without the fear of a court of judges. If the code is a bad one, it is not worth following, and will not be accepted in spite of any supervising committee, however great its authority. It must be remembered that no matter from what association or individual such a law of nomenclature has emanated, it is and will always be temporary. It is impossible to determine upon any rules that will stand for all time, because what meets the present needs will most likely not satisfy the next generation. How long, then,

shall a writer consider himself bound to follow these rules? They will certainly have to be changed from time to time. It is especially impossible to decide upon the fixity of special terms, because a name may be founded on ideas, which, in the course of time, owing to the progress of science, will be shown to be incorrect. No such rules as are applicable to the nomenclature of taxonomy can be brought into effect in regard to a system of terminology.

The law of priority, which is the first principle in the nomenclature of systematic biology, cannot be strictly adhered to in this connection. It has been proposed by CLEMENTS<sup>2</sup> that "priority of term and of application is to be regarded as the fundamental principle of phytogeographical nomenclature." ENGLER, who must be considered as better qualified than most men to judge in such a matter, in a footnote to CLEMENTS' article expresses strong objection to the introduction of a law of priority in phytogeography. The acceptance of such a law would lead to the retaining of names which are neither expressive of the idea they represent nor suitable in other ways. If an absolute rule of priority is maintained, how are we to arrange for the retaining of names that originally expressed ideas now considered as false? Every terminology shows traces of such names. What conception in that case shall represent the type of the systematist and bear the old name? It can be seen at a glance that the rule of priority is not practicable here as it may be in taxonomic nomenclature.

The question whether to retain an old term which is not good, or to abolish it and substitute a new name, will always be difficult. If a free hand is given, phytogeography will have a heavy load of useless synonyms that always will act as a drag on true science, and create much more confusion than exists now. If on the other hand any restriction can be brought about, it must be to the effect that priority should be conceded to such a name only as has been properly defined in a work accessible to scientists. To impose new names needlessly upon previously named conceptions will always be considered bad form, and a general consensus of opinion prevails as to this habit. Suddenly introducing a large number of new terms into

<sup>2</sup> CLEMENTS, F. E., A system of nomenclature for phytogeography. *Beiblatt Bot. Jahrb.* 70: — 20. 1902.



a new science is the best way to stifle it. It is with great hesitation that a new term should be coined, and it needs in each case a specialist to decide as to the necessity for such an action. Good and forcible reason should always be shown why an old term is not sufficient to indicate the conception that is to be described. It should never be forgotten in rejecting already established names that there is a possibility that the new term may meet a similar fate from a later writer. If that were always borne in mind, perhaps writers would think twice before entering the arena as name-makers. The true test of the quality of a term is generally the time it is able to exist, provided the conception as such remains unchanged. Not infrequently, however, names are introduced into a science—phytogeography not excepted—for speculative theories and ideas, upheld and supported by facts which are consciously or unconsciously misinterpreted to fit preconceived notions. In other cases new terms are proposed for already named conceptions, because of ignorance on the part of the writer. We may here remember what DECANDOLLE says in his *Phytographie*: “the perfectly honest and right-minded botanist may sometimes have failings. He may neglect to cite his predecessors, or cite them inexactly, either from negligence or from want of literary resources. The latter case may be deemed a misfortune and no fault.” “But,” continues DECANDOLLE, “if he has not the necessary books within his reach, why not go where they are and consult them? Or if unable to do that, why need he publish?” Where a writer may have enriched the nomenclature with a new term for which no need existed, the application by subsequent writers of the rule of priority is to be recommended. If the term in question be introduced by a writer who enjoys real or affected authority, and his term is accepted upon such motives by a thoughtless multitude, it will naturally sooner or later be suppressed or ignored and finally disappear.

When we undertake to revise nomenclature and find terms the meaning of which is doubtful, the only proper way out of the dilemma seems to be to ascertain the conception given to such terms by the original proposer. If the term cannot be used in that sense it should be discarded. We have a good illustration of this in the much mis-treated term “phytogeographic formation.” It was originally proposed

by GRISEBACH (1838) to designate an aggregation of plants characterized by a dominant species. But, as his examples show, GRISEBACH considered his formations as having a certain physiognomic aspect, and when in 1872 he moderated his conception of the term formation to an association characterized by a physiognomic type instead of by a dominant species, he only more pronouncedly brought forward the conception of a physiognomic unit. Leaving aside all the various uses of this term by later writers, we have to consider whether the original conception of GRISEBACH of a general plant-topographic or physiognomic unit, such as forest, steppe, tundra, or prairie, can be retained in the light of modern investigations. If that is the case the name stands, if not it falls. I have endeavored to show, in a paper now in print, that we need the term formation in the sense of GRISEBACH. Did our limits allow, we might call attention to many other instances where we could clear up the muddy stream of phytogeographical names. One more example will suffice to show how this rule would work. The word zone is now used as a technical term in phytogeography to designate at least the following conceptions: the successive belts of vegetation on a mountain side, the horizontal climatic zones of the surface of the earth, the belts of vegetation surrounding a pool or succeeding each other on a shore, the submerged belts especially of marine algae, the layers in a fossil-containing deposit; in many local descriptions it is adapted for designating any convenient floral area delimited from others; and finally in anatomy the term "zone" is applied to any area distinguished in structure from its surroundings. That this multiform interpretation of the word zone needs adjustment is manifest. In the technical language of a science a term should have only one meaning. Nothing but confusion will come from the admission of enigmatic terms, and the clarifying process is therefore the one we expect the nomenclature of phytogeography will shortly be exposed to. If in regard to the term zone we follow the principle given above, we have to ascertain what author first introduced it as a technical word, and in what meaning it was used by him. In 1839 BOISSIER designated with this term the vertical belts of plants in mountains. In a corresponding sense it had been used for a long time previously in topography, as also FLAHAULT<sup>3</sup> mentions. The

<sup>3</sup> *Projet de nomenclature phytogéographique*. 1890.

term zone in plant-geography, therefore, should signify the successive stages of vegetation from the base to the summit of a mountain, and nothing else. It is true that WAHLENBERG<sup>4</sup> in 1812 designated these belts with the term *regio*, and if we followed the rule of absolute priority, this would be the correct term. *Regio*, however, was used long before WAHLENBERG's time by botanical writers in the general sense of a geographical area of more or less definite extension, and so was zone. In this case we are confronted with two synonymous terms, and the only principle on which a decision can be based seems to be that of general usage. It must be admitted that it is an extremely difficult matter to lay down any rules that would take us out of dilemmas such as this. If it were possible to canvass the various authors to ascertain which term has been used more than the other to designate this special feature of mountain belts we are considering, it is very doubtful at what result we would arrive. *Region*, however, since MARTIUS used it in 1831 for a certain phytogeographical area, has generally been understood and adopted by the best writers for that purpose. FLAHAULT has made the relation and usage of these two terms, zone and region, clear by adopting them in the sense advocated above. If that is universally done, we have to find other appropriate terms for the various conceptions that often have been called zones. Nor need we take refuge to the method of making new terms in this case, for we only have to make a selection from the multitude of expressions already used, and in selecting we can make a choice that will serve in other languages as well as our own, and thus to some extent satisfy the call for an international nomenclature.

The first and most essential principle of nomenclature is clearness. To obtain this result, all the expressions used in technical terminology, whether they be old established names or newly coined ones, must be definite, concise, perfectly distinctive, and easily intelligible.

All names and terms are for the sake of convenience. In order to insure mutual intelligibility, greater precision, and clearness, it is imperative to avoid names that will create error or ambiguity. It is not inconceivable that the need of short compendious names and terms to denote phytogeographical facts or processes can be met

<sup>4</sup> Flora Lapponica. Berlin. 1812.

by individual monographers following certain general principles, which should be applied with all possible generality. *Festina lente* is the maxim into which we might condense the prevalent, but perhaps not yet outspoken condemnation of the tendency to drown our science in a torrent of unpronounceable so-called international terms, which cannot but embarrass the student, render the subject less accessible and more difficult to handle, and be exasperating to lovers of a clear, consistent, and uniform nomenclature.

Emphasis must also be laid upon the manner in which a term comprises the idea it is to convey to the reader. In systematic biology it is now held that a name need not contain any reference to the subject it represents, and may be wholly meaningless. This would hardly be convenient, however, in a system of terminology. The limitation of human memory makes it important that the term or name employed in a descriptive science should not be merely a name, but also associate in one form or another our thought with the subject we are discussing. In making new terms or in discriminating between already existing ones we should bear this in mind. It is just as easy to coin a name of this kind as it is to make a meaningless one. There might be a tendency to attribute too much importance to the meaning of a name, but all things considered it seems easier to remember a term that at once conveys to our mind the conception it stands for.

It has been recommended by several writers that we ought to avoid having names that are already used in geology or some other science nearly related to phytogeography. It stands to reason that such a course is neither absolutely necessary nor very advisable. Although we speak of stratification in connection with sedimentary processes in dynamic geology, it does not follow that the term stratification could not be used in plant geography to designate the division of a plant community into strata, without implying any ambiguity or causing any confusion. Objection has been made in regard to certain terms such as formation and province, the former word being used in geology, the latter in a political sense. If we were consistent, a great number of names which have been used for a long time in botany ought to be ruled out, because they are also used in zoology, or *vice versa*, as anatomy, cytology, heliotropism, parasitism. Any

small inconvenience that may result from this principle of ignoring the fact that a term is already established in another science would be counterbalanced by the appropriate use of similar terms to designate related phenomena in related sciences.

It is of importance in applying technical terms or inventing new names to take a broad view of the subject, and not use geographical terms, that generally refer to large areas, to signify local phenomena. We might mention as an example the use of the expression Austral zone for a phytogeographic area of North America. It has always been understood, however, that the term austral refers to the southern hemisphere, and it is as wrong to use the word in the way mentioned as it would be to apply its counterpart boreal to the northern part of Brazil or Australia. It would be greatly misleading if a botanist, say in Australia, would designate for instance the eastern coast region of that continent as the Oriental region.

When LINNAEUS brought about the reformation of systematic nomenclature he freed the names from the cumbrous descriptive phrases by assigning to each object a generic and a specific name. Similarly a concise mode of expression in phytogeography ought to be agreed upon, so as to save a great deal of verbosity which at present naturally must accompany an exact and complete phytogeographical description. The difficulty of presenting the results in a compact form would not be very much bettered, however, by adopting suddenly a number of new terms, because most likely the remedy would in that case be worse than the disease. It may be safely said that by instituting a uniform method of applying necessary terms, and by bringing such an agreement into universal practice a long step would have been taken towards establishing order.

The question of obtaining a nomenclature of an international character has been discussed to some extent. There can be no doubt as to the beneficial results that would follow the adoption of such names. The practicability of the application of any rule to that effect, however, seems somewhat doubtful. Be that as it may, we are justified, I think, in looking forward to some kind of tacit agreement in this case between plant-geographers of different countries.

Another question is how such international terms should be formed. WARBURG and CLEMENTS think that only Greek and Latin

can be used. FLAHAULT, NILSSON, WARMING, and ENGLER, among others, are of the opinion that vernacular names ought not to be excluded. While it seems absolutely imperative that in referring to plants we should use only the scientific name, it does not appear to be so overwhelmingly important to change all those terms of vernacular origin, which already are established in phytogeography, into quasi-international substitutes drawn from Greek or Latin. In the former case we have thousands of names, and consequently we use the accepted scientific names, which can be easily identified, instead of the vernacular, as the latter would surely give rise to confusion. On the other hand, the number of technical terms in phytogeography is fortunately not yet so great as to make the list a very voluminous one. Even if vernacular names are retained, or introduced to designate certain facts, this would not militate against a uniform nomenclature so long as the names are clear and do not give rise to any doubt as to their significance.

One fatal objection to a change into Greek-Latin of such commonly understood and accepted names as tundra, prairie, chaparral, scrub, savannah, and others, is that in spite of the adaptability of these ancient languages, it is impossible to translate these terms adequately, since the ancients did not have any conception of the ideas or facts these names represent, and any attempt to fabricate a modern name from the ancient languages to signify, for example, the formation known as the patana of Ceylon would be a failure, so long as we want the term to suggest to our mind the peculiar conditions that characterize this particular formation. If we consider the chief object of nomenclature to be to serve our convenience, I fail to see why the name patana would not be acceptable in any language, and thus be international. As a matter of fact, it is so already, and in all probability very few persons would approve of a Greek-Latin equivalent coined according to the principle of constructive naming. CLEMENTS, who is the principal advocate of the latter method, and who has augmented the labor of those who are endeavoring to find a way in the labyrinth of phytogeographical terms by proposing at least 500 new names, has given the name psilium to a prairie formation, deriving this "international" term from *ψιλῆιον* or *ψιλά*, bare, naked. Now this new name does not convey any idea of a prairie

to the reader because it can be applied as well to any treeless formation. *Prairie*, on the other hand, is a term well-known to every school-boy the world over, and there is no need whatever to overload memory with a new name that serves no useful purpose. For the term "bad lands" of Nebraska CLEMENTS suggests hydrotribium, and for plants on that formation hydrotribophyta. Terms such as these are very expressive in a way, but they are certainly not an improvement. The English "bad lands" applied to this particular formation is widely known, it causes no ambiguity, and there would be no objection raised against its acceptance in French, German, or any language, but most people would certainly protest against hydrotribium. And still this last term can be pronounced, but what about ptenothalophyta, rhoium, ammochthophilus, proodophytia, mesochthonophilus, chosen at random from CLEMENTS' catalogue? The terms rolling prairie, rolling foothill, rolling downs, and so on, can readily be adapted in any language, and be just as characteristic as if we translated them into some more or less high-sounding name derived from the Greek word for rolling, or wheel, or ball, or some similar expression. In geology many characteristic words have been borrowed from the vernacular for technical use, as fjord, atoll, and canyon. Would physiography have been better off in regard to clearness and brevity of expression if names of mixed Greek and Latin origin had been invented for these conceptions, which had no equivalent in the language of the ancients? ENGLER, in the footnote to CLEMENTS' article already referred to, gives the following categorical judgment in this matter: "dass es sich nicht empfiehlt, die volkstümlichen Bezeichnungen von Pflanzenformationen aus der pflanzengeographischen Literatur zu verbannen."

What has here been said may suffice to show that new names cannot be invented to advantage for features that already have well established and characteristic designations in the vernacular language of the country where they constitute a salient feature. Good common sense in this as in many other cases must be the guide in choosing technical expressions.

If a suggestion were offered as to the first step necessary in order to obtain uniformity, it would be that we have to decide about the various kinds of floristic, topographic, and ecologic units that can be

and are necessary to distinguish. It has been suggested<sup>5</sup> that the division of the vegetation into formations must be founded upon the concept of habitats. This principle is a good one, the only difficulty seeming to lie in the practical working of the rule. Any one conversant with the great variety of forms of habitat is aware that such a classification is no easy undertaking. In all attempts made the authors have decided for one or another environmental factor that has influenced the development of the formation, and consequently the classification has been more or less artificial. The task of identifying, classifying, and naming plant aggregations, or features of the vegetation, is extremely difficult because of the comprehensive data necessary to illustrate the complex factors influencing distributional phenomena. The use of one class of names that refer to habitat, however, are inevitable and absolutely necessary. For such terms we can turn to the vernacular language, which often possesses very expressive names that combine in one word the main features of environment. Together with the term formation as representing the large topographical units of vegetation such vernacular terms are very adequate. Let me give a few examples to illustrate this. The chaparral formation of California and southwestern United States generally is one of the most peculiar anywhere. There can be no doubt about the meaning and scope of the term, when the formation has once been clearly defined, because it has no counterpart in any other region of the world, although it certainly is paralleled in many places by related formations. The expression chaparral formation gives not only a general idea of the component plants, but it also includes a conception of the topographic aspect of the country where the formation occurs, and whose physiognomy it assists to mold. Still the term is strictly devoid of any reference to the dominant species concerned in the aggregation of plants in any part of the formation. Formational names should always be so. A formation can be subclassified into associations, and these into communities. The latter can be designated adequately by adding the suffix *etum* to the scientific name of the dominant plant after the method first suggested by HULT.<sup>6</sup> The limitations of this article do not allow me

<sup>5</sup> CLEMENTS, *l. c.*

<sup>6</sup> Försök till en analytisk behandling af växtformationerna. Medd. Soc. F. Fl. F. 8:1-155. 1881.



to enter into details with regard to this method of classification, which I have found works equally well in the arctic parts of Europe and in the Mediterranean countries; in the primitive tropical forests of Ceylon, northern Australia, and Polynesia, and in the semi-arid regions of New South Wales and Western Australia; in New Zealand and in California. I may say that in my work in these countries I have not found it necessary to introduce any new system of naming, but merely to coordinate and classify previously existing conceptions. And I firmly believe that this working out of the synonymy will be the only method by which a final agreement can be reached.

We have further to classify all the units of one kind or another into groups according to relationship, and to give names to them, availing ourselves as much as possible of terms already existing, the synonymy of which must be cleared up thoroughly. After laying down the general principles of nomenclature in the code to be recommended, we have to leave the application of these canons to the individual writers.

This should be the program for a permanent committee to be appointed by the next international congress. Let this body then publish the results of their work and submit them for leisurely consideration and discussion. When conflicting opinions, if there are any, have been expressed, and direct or circumstantial evidence has been brought in to illustrate and reinforce the various principles, it is time to settle the matter by adopting a general code of nomenclature. There can be no hope of getting any substantial improvement in existing conditions through any immediate action of the botanical congress, because of the great diversity of opinion and practice that prevails, and because no definite proposal based on facts and logical arguments has yet been held forth which could be made subject to a detailed criticism. Any proposition that presents principles or terms without proper and clear definitions can naturally not be considered.

The question may arise as to what constitutes a definite description. The degree of exactness and clearness of expression will naturally vary with the different authors, but so long as there remains any doubt as to the feature meant by the writer his term can hardly expect to be generally accepted.

*Nomina nuda* in the sense of systematic biologists appear not infrequently in phytogeographic literature, and it must always be considered as insufficient definition to supply merely a translation of a formational name, without giving a description sufficiently clear to remove every trace of doubt as to what the writer has described.

Whenever coining of pseudo-classical names is resorted to, it is to be expected that the author would at least take into consideration some degree of linguistic purity, besides the matter of precise meaning, because it is important that terms which are also to be spoken should be euphonious and in some harmony with the pronunciation.

In regard to the rules of coining new terms from Greek and Latin it has been claimed that the classical languages only should be considered. Rules of that kind are difficult to follow. In the real classical Latin, for example, the words are used in so many different ways that it will often be difficult to bring them into conformity with the primary rule of technical nomenclature that each idea should be represented by a single term only, and each name should have only one meaning. The classical Latin of botanists has been the Latin of Linnaeus, and it will most likely always remain so, because of its definiteness and conciseness. Whatever language is chosen, in the forming of new words we must follow the rules of the language; but we must also remember that by driving the systematizing too far we will only increase the difficulties, and by a too sedulous adherence to preconceived notions we might arrive at results which are not in unison with the true progress of science.

One important point is that in forming new terms for phytogeography we must avoid terms which already, in one form or another, are used in botany. To call an orchard formation dendrium will lead to difficulties, because that name is already used to designate a genus of plants. The same objection can be made to *eremia*, *amathia*, *lophia*, *petria*, *xylia*, and scores of other terms proposed by CLEMENTS.

The rule suggested by that author "that a term to be valid must be proposed by a botanist" is incongruous. In hazarding this criticism I must confess that it appears to be a hard rule that forbids any one who has facts to present concerning the vegetation or flora from doing so, provided he is able to express himself correctly, no

matter whether he claims the title of botanist or not. Or is it the coining of names only that should be restricted to botanists? Who is a botanist? Where shall the limit be drawn? Does knowledge of a certain number of plants entitle a man to this privilege? Or is publication of a certain number of pages on some botanical subject a sufficient qualification? If such a rule were accepted and applied, we should have to reject, for instance, the term "ecology," because it was first introduced by ERNST HAECKEL, who never claimed the name of a botanist, although he knew more about the subject than most "botanists."

Enough has been said upon this matter. We should take up a conservative position in this question of nomenclature, but at the same time insist upon the adoption of a code announcing certain principles, the application of which will prevent such a plentiful harvest of confusion as we have now, and assist in bringing about a reform resulting in a nomenclature better adapted to the needs of scientific workers. "Prove all things; hold fast that which is good" is the very essence of such a code.

To summarize the previous discussion:

Clearness and conciseness are the main requisites for a system of terminology.

Each technical term should have only one meaning.

In case of doubtful terms consult the proposer of the name. If the conception it represents is not absolutely clear, the name has no status in nomenclature.

If a term has been commonly used and understood in another sense than the original author proposed, it should be retained, but only in case there can be no doubt as to its interpretation.

If a conception has already received a name and there is no obvious reason to discard that name, an author has no right to propose a new term.

A law of priority is practicable, we think, only so far as the principles laid down in the previous pages of this article will admit.

A name, the conception of which has been materially changed in the course of time, naturally has no standing.

A technical term should be associated in our mind with the idea it represents.

A technical term should be defined clearly, so as to leave no doubt as to its significance. Authors should desist therefore from proposing new terms in mere catalogues.

A new term should be published in some work accessible to scientific workers.

Vernacular names should not be excluded from phytogeographical nomenclature, but they must in every case be definite and give rise to no ambiguity.

An international committee of phytogeographers should be appointed by the Vienna congress, to continue the work on a proposed code of rules.

This committee should consider what kinds of technical terms are needed; how they should be classified, for example with regard to distribution, abundance, elevation, phenological phenomena, etc.

The result of the work of the committee already existing, and of the succeeding one, should be published at an early date, so as to give the public ample time to discuss the various phases of the question, before the following congress assembles.

STANFORD UNIVERSITY, CALIFORNIA.

THE FORESTS OF THE FLATHEAD VALLEY, MONTANA.  
CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY.  
LXVII.

HARRY N. WHITFORD.

(WITH MAP AND TWENTY-THREE FIGURES)

[Continued from p. 122.]

II. EDAPHIC FORMATIONS IN FLATHEAD VALLEY.

IN the previous pages an attempt was made to show why the west side of the valley contains a prairie formation, and the east side a forest formation, and why the coniferous type of forest prevails rather than a broad-leaved deciduous type. A plot will now be presented in detail to show why in the forest formation there are some areas altogether without trees. In order to reach definite conclusions, a limited area was selected to represent the whole forest area of the valley. This area, comprising about 250 square kilometers, was mapped, and the conditions for forest growth were determined (*map*). The relation of this area to the whole valley is shown in *fig. 3*. It lies at the northeast end of Flathead Lake, and includes a portion of the main valley on the east side of the Flathead River at the head of the lake, the low end of the Mission Range of mountains, and a portion of Swan valley. In this area are found many types of topographic diversity, from Flathead Lake (890<sup>m</sup>) to the highest point (about 1372<sup>m</sup>) in that part of the Mission Range which is included in the map. No detailed study was made in the higher Swan Range east of the valley, though some conditions of tree growth were noted in these mountains. As shown by the map, five distinct edaphic formations were found: meadow (*hydrophytic*), Engelmann spruce (*meso-hydrophytic*), western larch-Douglas spruce (*mesophytic*), Douglas spruce-bull pine (*meso-xerophytic*), and prairie (*xerophytic*).

THE MEADOW FORMATIONS (HYDROPHYTIC).

As already mentioned, Swan valley was formerly a lake, the present condition being only a stage in its recession. The drainage consists of Swan Lake, Big Fork River, and a number of small

streams; also one large pond known as Ross (Mud) Lake, which, with its outlet Ross Creek and the numerous small inlets, comprise the drainage of the extreme north end of the valley.

The most noteworthy fact about the hydrophytic vegetation is its resemblance to that found in similar edaphic situations in the eastern United States, both types of swamps being found here. Near the head of Ross Lake is a sphagnum meadow, in which *Menyanthes trifoliata*, *Drosera rotundifolia*, *Comarum palustre*, *Eriophorum polystachyon*, and *Betula pumila* are characteristic. At least two other large meadows show this combination. One of these is along Little Bear Creek, and is known as the School Meadow; another is found along Flathead River, and will be discussed in connection with the spruce forest which lies close to it. Ross Lake (fig. 9) is a pond which shows very well the zonal distribution of plants, being shallow and with a very muddy bottom. In its center and in streams bordering it are found the following characteristic species: *Nymphaea advena*, *Brasenia purpurea*, four species of *Potamogeton*, *Myriophyllum*, and *Hippuris*. The sedge zone bordering the water of the shallow ponds and streams contains the following species: *Bromus Richardsonii pallida*, *Muhlenbergia racemosa*, *Carex utriculata*, *C. viridula*, *C. hystericina*, *Calamagrostis caespitosa*, *Phalaris arundinacea*, *Juncus Regelii*, *Scirpus lacustris occidentalis*, *Lobelia* sp., *Cicuta maculata*, *Solidago* sp., and *Dodecatheon* sp.

The meadows are usually submerged during the spring and early summer months, when the melting snow of the mountains to the east swells the streams, and brings the water level slightly above the surface. In the latter part of the summer and fall the underground water level is a little below the surface; and it is this condition of submergence and emergence that determines the meadows and excludes trees. Of course some of these meadows are never entirely submerged, but are always wet, with few exceptions being associated with streams. The largest meadows are found near the head of Ross Lake, at its foot on the east side, near the mouth of Wolf Creek, at the foot of Swan Range along Little Bear Creek, and in the large bend of the river just east of Swan River cañon.

The meadows are given brief mention here in connection with this forest study because they are genetically related to the spruce

forests that usually border them. It is obvious that trees do not grow in them because the amount of moisture in the soil is too great. Some of the meadows have been artificially drained, others have been planted to timothy, and one in particular, in the northwestern corner of the area (*map*), has been drained and cultivated for a number of years, so that its former nature was discovered with difficulty. What has been done artificially is being done naturally, but more slowly. The detritus that is washed into the ponds and the vegetation that dies down from year to year are filling up these bodies of water, and are making the meadow condition possible. Again, the streams are cutting their channels deeper, thus lowering the underground water level at their borders, and this changes conditions that favor meadows and introduces those that make the forest possible. It is very probable that many areas now occupied by spruce and other forests were formerly occupied by meadows. Indeed, all stages of development towards this forest condition were noted, and will be discussed under the next head.

#### THE SPRUCE FORMATIONS (MESO-HYDROPHYTIC).

In many places species of *Salix* and *Alnus incana* encroach upon the meadows, sometimes forming dense breastworks around the grass areas, so that it is difficult for other trees to get a start. This is the case when the zones of underground water level are sharply and narrowly marked off. Usually, however, when the underground water level is at a fairly uniform distance below the surface for a rather broad area, as it is where the small streams spread out over a level extent of land, the willow-alder breastwork is absent. These situations are favorable for the advance of *Picea Engelmanni* into the meadows. The youngest trees are found on the hummocks in the meadows; nearer its borders are the older ones, though they are still scattered; these grade imperceptibly sometimes into dense forests of spruce, many of the trees reaching huge dimensions. Since this formation is found best developed on situations where the underground water level is a little farther below the surface than it is in the meadows, it may be called the meso-hydrophytic formation.

It must not be supposed that there are no other trees with the spruce; indeed there are only small tracts where pure spruce woods

are found. The most common companion trees are *Populus angustifolia*, *Populus tremuloides*, and *Betula papyrifera*. These species nearly always form a small per cent. of the spruce forests, and in the meso-hydrophytic area along the Flathead River they occupy nearly the entire space. In Swan valley the soil is a mixture of clay and humus; along Flathead River, especially in the delta region, the subsoil is sand, overlaid by a fine alluvial deposit. In the dense woods the undergrowth is scanty, sometimes only one or two species being present, the most common plant associated with the pure spruce growths being *Rhamnus alnifolia*, although *Cornus stolonifera* is often found. In the narrow strip of this forest along the streams nearer the mountain *Echinopanax horridum* and *Veratrum californicum* are present. Since the spruce woods are transitional between the meadow and the mesophytic woods, the undergrowth of these associations is often present. Thus, near the meadow side of the forest, grass plots are frequently present, and on hummocks between anastomosing channels *Lysichiton kamtschaticensis* is frequent. On the other hand, toward the mesophytic side of the forest the elements of the undergrowth of the western larch-Douglas spruce formation are to be found.

An area of spruce is found in connection with a meadow in the northwestern corner of the plot not far from the Flathead River. Here on the border of the prairie formation is an area that has almost identically the same plants as the spruce forest in the Swan valley. Along the east side of this swamp there are numerous springs, some large enough to give rise to small streams, and others hardly noticeable. The source of the water supply is thought to be Echo Lake, which, with a number of smaller ones, lies in the depressions of a moraine that extends beyond the limits of the plot to the northeast. Save a small stream, there is no visible inlet to this lake, and its source of water supply is probably by underground seepage from the mountains that lie northeast. There is also no outlet above ground, and since the drainage is toward the Flathead River it is thought that the springs mentioned are fed by underground seepage from these lakes and ponds. This underground water level, as shown by the wells in the neighborhood, is in places nearly a hundred feet below the surface, and extends underneath the larch-Douglas spruce



and bull pine forests and the prairie to a low ridge near the Flathead River, where it issues in the form of springs, making conditions favorable for an Engelmänn spruce formation. Thus a bit of forest is projected, as it were, into the prairie formation. Where the water level comes nearer the surface the meadow already mentioned is associated with the forest.

Another meso-hydrophytic forest in which the spruce is almost entirely wanting needs to be mentioned. Around the head of Flathead Lake, including the delta at the mouth of the river (figs. 1 and 4), and extending up the river from its mouth, is a region that is annually submerged.<sup>13</sup> This region is occupied by a dense growth of willows, cottonwoods, birch, aspen, and other trees. On each side of the mouth of the river are long, low peninsulas of sand, the ends of which are entirely barren of vegetation. These are above water only a short time during the growing season, and this fact no doubt prevents plants from getting a start. A short distance back from the end of the delta on a little higher land is *Salix fluviatilis*, in some places so thick as to be almost impenetrable. Underground stems are sent out from this center, and thus new territory is gradually conquered, so that as fast as the delta is built out it is occupied by this pioneer willow, which prepares the way for changes that make it possible for higher forms to exist. When the water is high its contact with the willows causes a deposit of fine silt, so that the delta is gradually built higher and higher, making conditions favorable for the growth of such plants as the red dogwood, other species of willow, narrow-leaved cottonwood, paper birch, aspen, choke cherry, two species of hawthorn, and service berry.

Around the head of the lake there is a low terrace which is also submerged in the spring and early summer months. Instead of *Salix fluviatilis* there is a thicket of other willows; and on the lake side of this there are a few scattered specimens of *S. fluviatilis* and *S. amygdaloides*. On the land side of the willow thicket are the birch,

<sup>13</sup> During the spring and early summer months Flathead Lake and River rise some 4 to 6m, submerging all the surrounding low country. In some instances excessive floods do great damage to the country lying at the head of the lake. Since nearly all streams in the valley have their sources in the mountains to the east, the deforestation of this region would greatly increase these spring floods and greater damage would be the result.

cottonwood, and aspen; and here and there are found small patches or single specimens of the western larch, Engelmann spruce, Douglas spruce, and bull pine. None of these were noticed on the delta proper, and with the exception of the Engelmann spruce they seldom occupy the areas that are often submerged. Of course in the lowest places the meadow type of vegetation prevails, and elements of it are scattered more or less through the area occupied by the trees. As already shown, the lake formerly extended over the valley north of it, and as its waters receded it is very probable that vegetation similar to that found around its shores today occupied similar areas around the shore line of the former lake. Of course as the gradual lowering of the underground water level brings about unfavorable conditions for those plants that exist around the shores, these are replaced by those needing other conditions. On that portion of the shore line that borders the area where the rainfall is insufficient to support trees, the swampy areas will pass through the meadow, the cottonwood-birch-aspen type, to the prairie. However, if the shore line be in a region that has sufficient rainfall to support a forest, the first two stages will be followed by a western larch-Douglas spruce-bull pine stage.

Since the Engelmann spruce is the most prevalent and the most important tree in the formation just described, its silvicultural habits will be summarized. It has been shown that it does best in soils where the underground water level is not far below the surface, that is, for the plot under consideration, in low-lying lands bordering lakes, ponds, or streams. Thus it occurs not only in Swan valley, but also along the banks of Flathead River, where it is somewhat sparingly mixed with cottonwood-birch-aspen groups. It is the first tree to advance into the meadows. However, the Engelmann spruce is not confined to the more or less swampy region, for it is found scattered through the mesophytic areas in Swan valley. In the stands that lie adjacent to the spruce forests it is almost always present, and in some places it extends well out into the drier parts of the western larch-Douglas spruce formation, being found beyond the limits of the silver pine and lowland fir, and having a wider life range than either of these two species. It was often observed in the bull pine-Douglas spruce association where depressions in the topog-

raphy brought the surface of the soil near the underground water level, and along streams. However, trees in these situations seldom reach large dimensions.

The Engelmann spruce can tolerate shade fairly well; in this respect it is different from western larch and Douglas spruce and is classed with silver pine and lowland fir. The fact that it can endure shade probably accounts for the presence of its seedlings in the forests that occupy the drier areas in the plot, for the forest canopy in these situations brings about a local climate that makes it possible for trees to exist that could not otherwise do so. The Engelmann spruce has the power of germinating in the open if there is sufficient soil moisture, and like the other shade-enduring species it does better in these situations than in the shade.

It will be seen from the foregoing that outside the semi-hydrophytic conditions Engelmann spruce does not flourish in the plot under discussion, being confined to the level stretches of land bordering on the meadows and open bodies of water. There is little doubt that as the waters of the former Swan Lake withdrew, meadows first occupied these areas and then were replaced by spruce stands. Just as the meadow conditions may be considered the first stage in the development toward the climax forest of the region, so the spruce forest may be considered the second stage. As the channel of Swan River is cut deeper the water level of the valley will be lowered, thus bringing about a condition favorable to the development of other types of forest which will replace the spruce association.

In the above account the distribution of the Engelmann spruce is discussed only in the area mapped. In the mountains bordering the area on the east it shows a wide altitudinal range, but is always associated with good moisture conditions, for it is found best developed in the damp cañons and on damp slopes where it is invariably associated with *Abies lasiocarpa*. In the high basins it does not do so well as the fir, but in the lower valleys it flourishes where the alpine fir does not.

#### THE WESTERN LARCH-DOUGLAS SPRUCE FORMATIONS (MESOPHYTIC).

In the discussion of the Engelmann spruce formation it was shown that on its borders and on the dry hummocks in stands of this tree other trees obtained a foothold. Just as there is a gradation from

the meadows into the meso-hydrophytic forest in which the Engelmann spruce predominates, so there is a similar change from these into a forest in which the western larch and Douglas spruce are the principal trees. Again, this difference is due to a change in the underground water level; in the meadows it is near the surface; in the Engelmann spruce stands it is slightly below the surface; and in the western larch-Douglas spruce combinations it is still farther below. Indeed, in this association the water level is so far below the surface in places that the roots of the trees do not reach it, but rather depend on the water in the surface layers that comes from the rains or by capillarity from the underground water level. Since there is a medium condition of water in the soil, the forests occupying these areas are known as the mesophytic formations (fig. 8). Other trees found with *Larix occidentalis* and *Pseudotsuga taxifolia* are *Pinus Murrayana*, *Abies grandis*, *Pinus monticola*, *Picea Engelmanni*, *Thuja plicata*, and occasionally *Abies lasiocarpa*, *Pinus ponderosa*, and *Tsuga heterophylla*; also certain deciduous trees.

Associated closely with the spruce and almost invariably surrounding stands of it, except where the lodgepole pine is present, is found a forest in which the silver pine and lowland fir are at their best. Thus on the west side of the bay-like area of meso-hydrophytic forest west of Ross Lake, the spruce is gradually replaced by a magnificent growth of lowland fir, silver pine, western larch, and Douglas spruce. The lodgepole pine occupies a good deal of the spruce stands that would otherwise have developed into a forest like that just mentioned, were it not for the influence of fires. In various other areas are found forests in which silver pine and lowland fir form a more or less conspicuous element, especially in the area near the mouth of Meadow Creek. They are never unaccompanied by other species and seldom become the dominant trees, probably because the climate is not so congenial to them here as to some of the other dominant species.

The silver pine closely resembles its relative the eastern white pine. As already stated, in Flathead valley it does its best in the conditions surrounding the spruce stands, or where the water level is not far below the surface. However, it spreads over nearly all the mesophytic region in Swan River valley and ascends the east slope

of the Mission Mountains in moist situations. In the swampy soils silver pine has a shallow root system and is easily blown over by winds, many large trees being observed lying prostrate with nearly the entire root system exposed. Where the soil has sufficient moisture, this tree can germinate in the open with no shade whatever, but it can pass the seedling stage in rather shaded conditions. The only two trees that have a shade too dense for it are the giant arbovitae and the western hemlock. While it can exist in the shade around the drier edges of the mesophytic forest, it fails utterly to maintain a stand in the mature growth of these areas, and except in extremely favored places the silver pine cannot be considered a successful tree for the region under consideration. It succumbs easily to fires, many instances being noted where fires had swept through the forests destroying the silver pine, while such trees as western larch and Douglas spruce were only slightly damaged.

The distribution of lowland fir is very much like that of silver pine, both reaching their climax growth in about the same situations. Where the water level is rather far from the surface it is more successful than silver pine in the low altitudes; but its altitudinal range is less than that of the latter. It is able to develop in open places, in soil so dry that silver pine is excluded. Where the moisture was sufficient it was not an uncommon thing to find stands of small (3 to 5<sup>m</sup> high) trees so dense that absolutely all vegetation was lacking beneath them. It is more tolerant of the shade than is silver pine, and because it can grow in drier soils it extends as undergrowth into the borders of the meso-xerophytic regions, where silver pine is seldom if ever found. Like silver pine and Engelmann spruce, the range of this tree is extended because of the protection of the forest canopy, but this is not the region of its best development. The largest trees seen were less than a meter in diameter and not more than 38<sup>m</sup> in height. SARGENT reports that it attains its best development along the Pacific coast in Washington, Oregon, and northern California, where it is frequently 75-90<sup>m</sup> in height.

By far the most successful tree in Flathead valley is western larch. It is a tree that closely resembles its eastern relative (*Larix laricina*) in general appearance, although its habits are decidedly different (fig. 11). As already shown, it is one of the first trees to gain a foot-

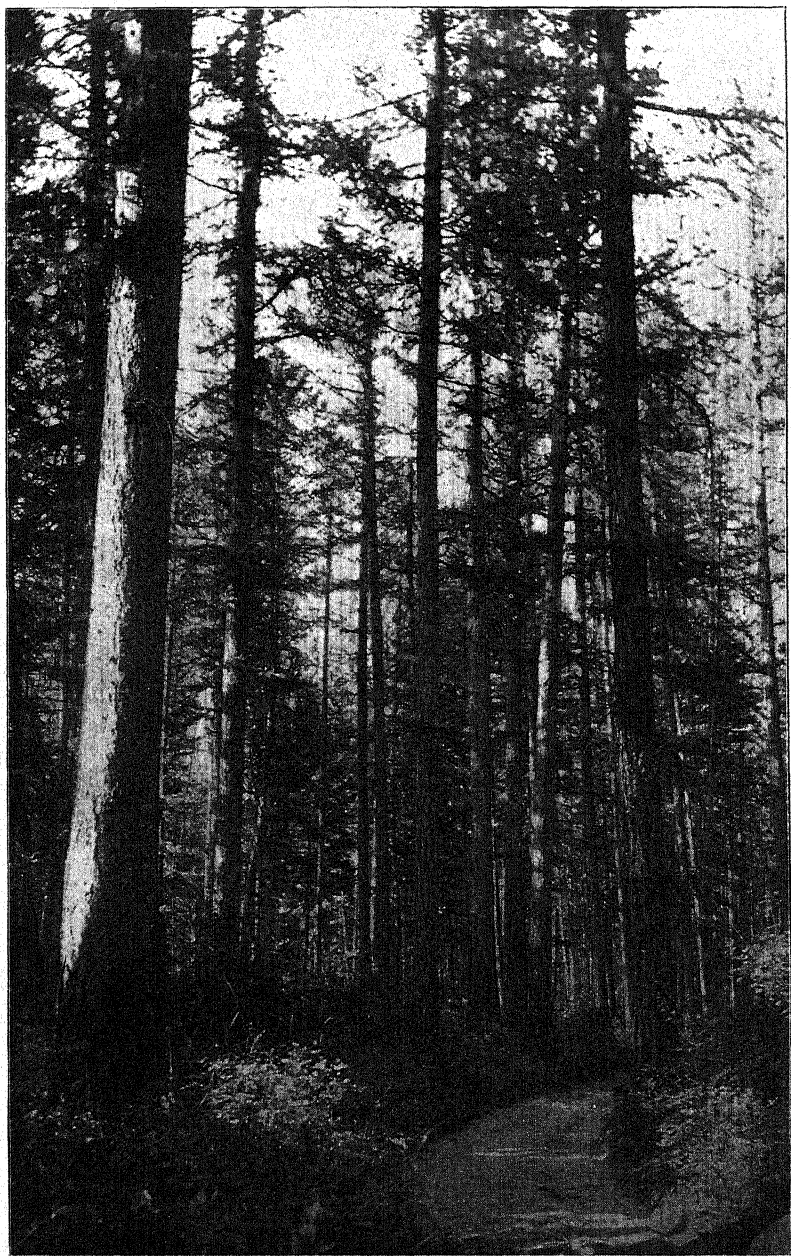


FIG. 11.—View of interior of a western larch-Douglas spruce forest near Big Fork, Montana; the undergrowth consists of *Acer glabrum*, *Philadelphus Lewisii*, *Holodiscus ariaefolia*, etc.—From photograph by McCALLUM.

hold in the spruce association, where it is found on the ridges and hillocks, and it forms an important element in the neighboring forests. There are extensive areas in Swan valley where this is decidedly the predominating species, and on the west slope of the Mission Range in some places there are almost pure stands. It extends out into the prairie regions along the river courses and on protected slopes. It does not grow in as dry soils as Douglas spruce and bull pine, and hence is more restricted in its distribution in regions where the rainfall is slight. The young trees, unlike those of silver pine and lowland fir, cannot endure shade. In no instance was a seedling observed growing in the shade of a forest. Other things being equal, it does best in broad open places, although it can do fairly well in slight openings where the sunlight enters at least during the middle of the day. The western larch then does not tolerate shade and cannot reproduce itself unless an opening be made first in the forest. This may be done in the mature primeval forest by the dropping out of old trees, but more frequently accidents such as fires and winds bring about open places suitable for its reproduction, provided of course seed-bearing trees are left to stock the soil with seeds. In contrast with silver pine and lowland fir, it may be called a fire-resisting tree. Its thick bark enables it to withstand fires that would kill silver pine and lowland fir, old trees often being found still living in the midst of burned areas. Sometimes isolated trees stand towering over the young lodgepole pine growth that has come in after fires (*fig. 12*), and the only young trees competing with lodgepole pines are western larch.

Observations on the rooting habits of trees are in any case difficult to obtain, unless windfalls are frequent. Many trees of western larch were found standing in windfalls where silver pine, lowland fir, and Engelmann spruce had been blown over. From this one would judge that its roots penetrate much deeper than the roots of these trees; indeed this may be one of the reasons why western larch is able to exist in drier areas than can some other trees, for a deep root system will enable it to reach nearer to the underground water level or at least below the superficial dry surface layers where a tree with shallow roots could not get sufficient moisture.

Since Douglas spruce is a successful tree in the regions bordering



on the prairie, a discussion of its silvicultural habits will be deferred until the meso-xerophytic forest is described. It is almost invariably



FIG. 12.—Three generations of forests in a "burn" near Ross Lake; first generation represented by isolated old specimens of western larch; second generation consists of a forest of lodgepole pines mixed with a few individuals of western larch; in the foreground is the third generation, which consists almost entirely of young trees of lodgepole pines.—From photograph by PRAEGER.

a companion of western larch in the mesophytic area, hence the name western larch-Douglas spruce association.



The giant arborvitae is another tree that needs brief mention here. In the plot under discussion, along the base of the Swan Range there are three isolated places where the arborvitae was noted. It is usually found in moist places and probably ought to be considered as a meso-hydrophytic rather than a mesophytic tree (*fig. 13*). West of the Cascade Mountains, where it reaches its greatest development, it is distinctly a tree of the moister regions.

Another tree found in Swan valley is alpine fir, mentioned before as associated with Engelmann spruce in the moist cañons of the mountains. From here it spreads to the subalpine regions where it occupies a prominent place in the basins where snow lies all the year. In places it also finds its way into the lower altitudes in rather moist situations, as in Swan valley. The birch maintains a place throughout the mesophytic area; especially is it frequent in the moister situations and mixed with the lodgepole forests.

The soil in the mesophytic area is variable in nature, the character of the vegetation changing to a certain extent with the variations. It is probably not the chemical composition that determines the kind of forest, but rather the physical composition, the capacity of the soil for holding water being the controlling factor. If the underground water level is not far below the surface, it makes little difference whether the soil is sand, clay, or gravel, so long as there is sufficient humus to furnish the needed nitrates. However, back from the low-lying lands, where the water level is too far below the surface to be reached by the roots of the trees, the physical character of the soil plays an important rôle. As a rule the soil of the valley is made up of clay, probably derived from the decay of the dolomitic shale, the principal rock of the surrounding mountains. This has been washed in and deposited in the bed of the former more extended Swan Lake, and is mixed more or less with silt. Humus has accumulated in places, and this is more abundant where fires have not been so prevalent; for not only do fires destroy the humus, but in the open places left after the destruction of the forest it dries out rapidly. In contrast with the rich beech and maple woods of the eastern United States, the humus content of the soil is considerably less in these coniferous forests. This is of course due to the fact that the needle leaf of the conifers is not so good a humus producer as the

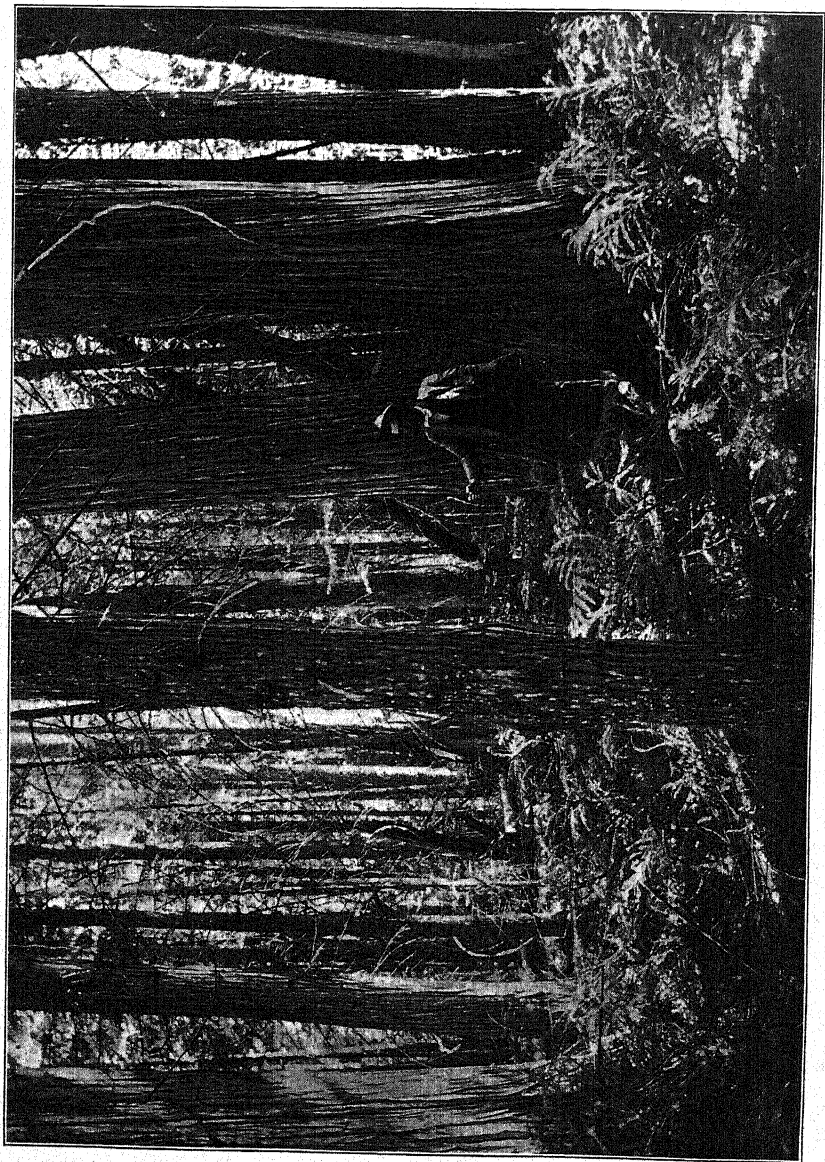


FIG. 13.—Giant arborvitae forest in an inlet of Sinyalcamin Lake, in a part of the Mission Mountains not in the plot mapped; the young trees under the old stand are all arborvitae, as no other species can exist in so dense a shade.—From photograph by HAMILTON.

broad leaves of the maple, beech, and other deciduous trees. In places, however, considerable quantities of humus are present, especially where the trunks of fallen trees have been allowed to decay and have not been destroyed by fire. A very good indication of a soil rich in humus is the number of species of fungi and mycotrophic seed plants found in it; *Monotropa uniflora*, *Pterospora Andromeda*, and *Corallorhiza multiflora* being scattered rather thickly throughout the forest. However, one misses the rich array of fleshy fungi found so abundantly in the leaf mold of the deciduous forests. Except in those places where arborvitae, hemlock, and lowland fir are prominent, the shade is not very dense; and under the rather thin canopy of the other conifers there is enough light to permit the development of a number of semi-shade species.

A woody plant that gives a decided tone to the undergrowth throughout the mesophytic area and to some extent in the meso-xerophytic area is the dwarf maple (*Acer glabrum*), the only representative of the maples found in Flathead valley. It can hardly be called a tree, for it seldom becomes more than 3<sup>m</sup> in height. Other characteristic shrubby plants are *Salix* sp., *Philadelphus Lewisii*, *Holodiscus ariaefolia*, *Amelanchier alnifolia*, and *Symphoricarpos* sp. In some places, usually more mesophytic, *Menziesia urceolaris* and *Taxus brevifolia* are found. Some of the forms, like snowberry, service berry, and mock orange, become more frequent as the forest becomes more open. Among the prominent more lowly forms were noted the following: *Berberis aquifolium*, *Aralia nudicaulis*, *Cornus canadensis*, *Chimaphila umbellata*, *Pyrola rotundifolia*, *Linnaea borealis*, *Rubus parviflorus*, *Clintonia uniflora*, *Adenocaulon bicolor*, *Tiarella unifoliata*, *Lycopodium* sp., and *Disporum* sp.

At the south end of Swan Lake, on the west side of Big Fork River, is an area with a soil decidedly pebbly, and probably of glacial origin (*map*), its inability to hold water being indicated by the character of the forest it supports. The Douglas spruce is about the only mesophytic tree found here, and in places there are groves of bull pine. On the east side of the river, so persistent is the absence of other species than Douglas spruce and bull pine, that the area was mapped as meso-xerophytic forest rather than mesophytic. It is rather open, and the vegetation in it becomes somewhat prairie-like;

indeed everywhere that the mesophytic forest grades into the Douglas spruce-bull pine combination the forest floor has prairie plants rather than forest forms.

It has been shown that the western larch-Douglas spruce association is found in those areas where the amount of water in the soil is less than in the areas that support the spruce formation. Again, attention must be called to the fact that in the former extension of the lake many parts of the valley now having mesophytic forest were moist enough to support spruce forests, and as the water of the lake receded the amount of water in the soil became less and less until the encroaching mesophytic forests crowded out the spruce forests. As there is a relation in origin, therefore, between the meadows and the spruce forests, so there is also a genetic relation between the spruce forests and the western larch-Douglas spruce forests. In places where the hills end precipitously near the lake shore, as on the west side of Swan Lake for instance (*map*), this relation is not so apparent, for the mesophytic forests reach in many cases to the water's edge. Yet even here narrow, flat areas at the foot of the mountains on the borders of the lake have small meadows with scattered Engelmann spruce and cottonwood in them. These will give way, of course, to the encroaching mesophytic element when the waters of the lake have further withdrawn.

In conclusion it may be pointed out that the climax forest of the plot under consideration is the western larch-Douglas spruce formation. This association occupies a greater portion of the comparatively level stretches of Swan River valley (*fig. 8*). It also is found on the protected slopes and foothills of the low Swan Range. No attempt was made to determine its range outside of the region mapped. The trees that are characteristic of this forest are western larch, Douglas spruce, silver pine, lowland fir, Engelmann spruce, and lodgepole pine.

THE DOUGLAS SPRUCE-BULL PINE (MESO-XEROPHYTIC) AND THE  
PRAIRIE (XEROPHYTIC) FORMATIONS.

Since the Douglas spruce-bull pine associations and the prairie are more or less connected, they will be treated together. A reference to the map will show that a rectangular plot of ground known

as Nigger Prairie lies just north of Swan Hill, at present used for farming purposes. It is bordered on the south, east, and west by narrow strips of pure bull pine forests, and on the north a forest of



FIG. 14.—View of bull pine forest south of Echo Lake; in the center is a large bull pine, the younger growth around consists of bull pine with some Douglas spruce. —From photograph by PRAEGER.

the same species extends to Echo Lake (*fig. 14*). This bull pine stand is surrounded on all sides by a mesophytic forest in which western larch and Douglas spruce almost entirely replace bull pine.

The question arises, what is the cause of this difference in the character of the vegetation in so limited an area? So far as could be ascertained, trees have been absent from Nigger Prairie for at least twenty years, and it is very probable that it has never been forested.

The character of the soil in both the prairie and the bull pine zone surrounding it is decidedly different from that of the country immediately adjacent. That to the south and west is a residual clay from the dolomite shale of Swan Hill; that to the east is a clay rich in humus; and that to the northwest, north, and northeast is a pebbly clay of glacial origin. On the other hand, the soil of the entire prairie and bull pine region is composed of sand mixed in places with a considerable amount of humus. The limits of this sandy area extend a little beyond the limits of the bull pine forest. It seems very probable that the absence of any other trees than bull pine is due chiefly to the physical character of the soil. It must be remembered that the climate of the area under discussion is such as barely to favor a forest, and a slight difference in the amount of water which the soil can hold may lead to the exclusion of certain trees, and in places of all trees. Since a sandy soil lets water drain through it readily, it is very likely that this area is too dry to support a mesophytic forest. As shown by wells, the underground water level in Nigger Prairie is some distance below the surface, so that those trees which have shallow root systems would not be so likely to succeed as those whose root systems are extensive and deep. The bull pine is one of the latter kind, and it is very likely that this is one reason why it has the habit of growing in drier situations than some of the other trees.

If the surface layers of a sandy soil can be made to retain water, the objectionable feature of such a soil will be partly overcome, and this can be brought about by an accumulation of humus. Lower forms of vegetation, even grass, by their decay will add to the humus content of the soil. In very dry countries this accretion would be exceedingly slow, for the oxidation of the organic débris would be great; but even in dry situations by the accumulation of a slight amount of humus the water-holding capacity of the soil might be increased sufficiently to tide a few trees over the driest months of the year. Trees once established in this way would help accumulate



humus more rapidly, for by fall of the dead limbs and leaves more organic material would be added than from the decay of lower forms of vegetation. The shade of the trees thus established would check the rapid oxidation of the organic material that takes place in the open. The ultimate effect would be the establishment of a forest in a place that was formerly occupied by a prairie. It is very probable that the whole yellow pine area just described was at one time occupied by a prairie vegetation. There is evidence that the present prairie island in this forest would become covered with forest trees if not interfered with by man, for along the roadside groups of young growth of bull pine seedlings are not uncommon. All around the border of the prairie young trees are present, and even in a timothy field there were noted seedlings that had escaped being cut by the mowing machine. Before the prairie island was settled it is very probable that surface fires swept it occasionally and thus checked the conquering of the prairie by the forest. Another prairie area similar to the one just described lies directly west of Echo Lake (*map*). Again, west of Nigger Prairie, just across the low range of Mission Mountains, is another "sand pocket" that has a prairie vegetation. These however border on the prairie climate.

The question arises whether the presence of bull pine will in any way change the conditions sufficiently to make them capable of supporting other species of trees. It was shown that the humus content of the soil increases more rapidly when trees are present than when they are absent. With the gradual increment of organic decay, it is very possible that the water-holding capacity of the soil may be increased to such an extent that it will be rendered capable of supporting other species of trees.

A bull pine seedling does not tolerate shade; the young tree must have broad open places where the sun strikes the soil a greater portion of the day. An opening in the forest made by the removal of one or two trees does not allow sufficient light and heat to enter; thus young stands are excluded from anything like a tolerably thick growth of these trees. This is not the case with western larch and Douglas spruce; it has been shown that the former does not tolerate shade, but grows in slight openings in the forest; the latter is very similar in this respect to western larch. If humus has accumulated

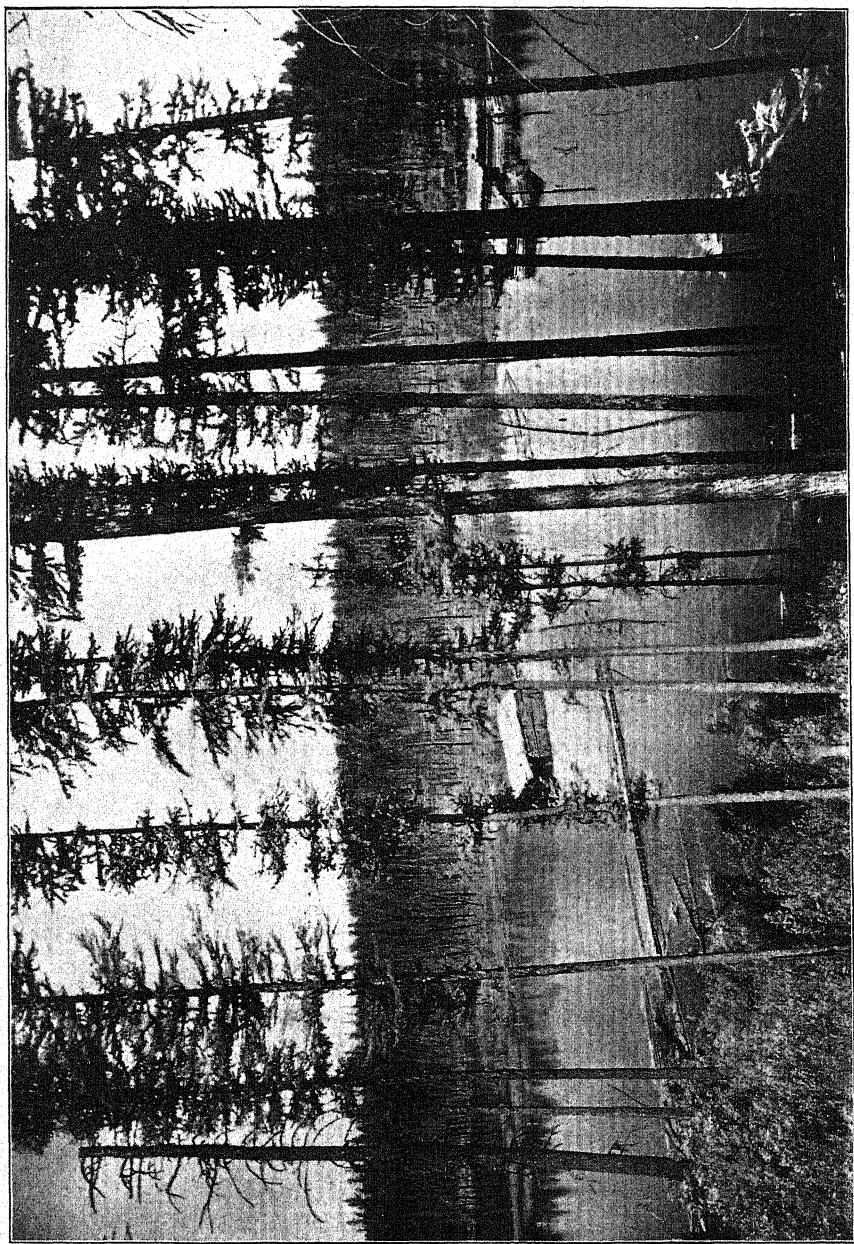


FIG. 15.—View of an arm of Echo Lake, showing submerged cabin and timber land; a few years ago this was dry land; the trees in the foreground are western larch and Douglas spruce.



so as to give the soil a sufficient water-holding capacity, open places in the bull pine forest may permit seedlings of both the species named to thrive. Numerous instances of this were noted in the bull pine forest under consideration. In places where bull pine had been removed there were clumps of young trees of Douglas spruce and western larch. If the place is sufficiently open, bull pine seedlings are found with the others. It will be seen readily that such a condition will lead to a gradual replacement of the bull pine forest by the Douglas spruce-western larch combination. There is some evidence that such a succession has already taken place, for all around the borders of the "sandy pockets" western larch and Douglas spruce are more numerous in places than bull pine. There is also reason to believe that in the pebbly clay morainic soil around Echo Lake, especially to the south and northwest, a more or less pure bull pine stand preceded the present stand consisting of a mixture of the three species. The bull pines are found in groups, or solitary full-grown specimens overtop the younger growths of the next generation of Douglas spruce and western larch, these isolated specimens doubtless representing all that is left of the former pure bull pine stand. Of course this succession has been a gradual one, occupying many generations, the more successful trees elbowing their way, as it were, among the less successful until the spread of the latter is limited by their incapacity to adapt themselves to the new environment. All stages in this succession are present today in the forest under discussion, and it was the study of these stages that led to the conclusion that has been advanced.

Out towards Flathead River the zone between the prairie and the forest contains a few scattered specimens of bull pine; next to this there is a more dense stand of this species with a few scattered trees of Douglas spruce; back farther still from the prairie is a zone in which bull pine is less and Douglas spruce more frequent; and finally another condition is found in which western larch joins these two species, bull pine being the least conspicuous element of the three. Such an arrangement is approximated just west of Echo Lake. This region is decidedly morainic in its character, and where depressions approach the underground water level western larch becomes more numerous, and in places near Echo Lake the surface

of these depressions comes near enough to the water level to permit the growth of scattered Engelmann spruce. This level of underground water varies, and this change is shown in the rise of the lake itself and the ponds around it (fig. 15).

Mention has already been made of the western larch-Douglas spruce combinations on the protected slopes of the Mission Moun-

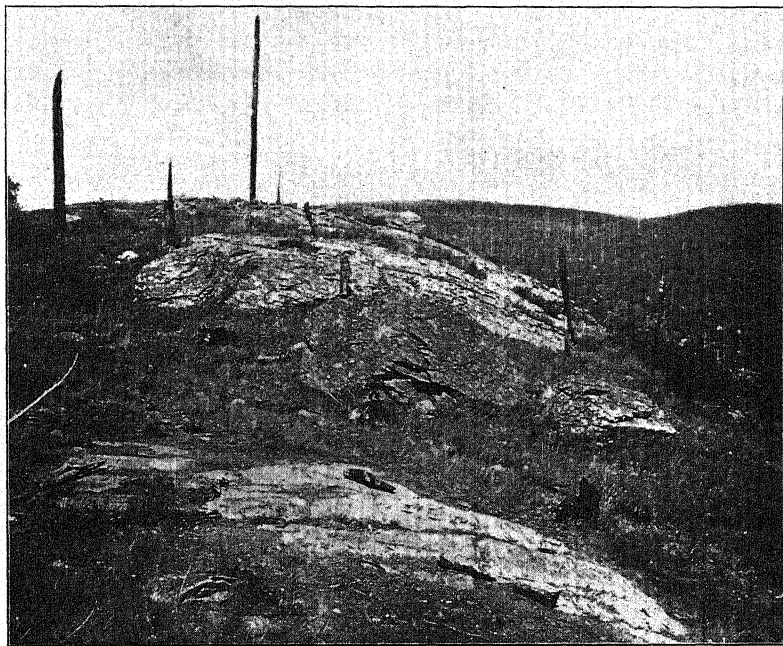


FIG. 16.—View on the top of the Mission Mountains showing area on which the Douglas spruce-bull pine forest has been destroyed by fire; the outcrop of dolomitic shale has been scoured smooth by the action of glacial ice; *Ceanothus* bushes on the right, lichens of various sorts on the rocks, and prairie grasses where the soil is sufficiently deep.—From photograph by PRAEGER.

tains. Toward the top of this slope western larch becomes less and Douglas spruce more prominent; in places the latter is mixed with lodgepole pine. On the west side of the range Douglas spruce and bull pine are the principal species; hence this area has been mapped as meso-xerophytic, although western larch is present in some situations.

The altitude of the Mission Range within the limits of the plot is nowhere more than 1372<sup>m</sup> above the level of the surrounding country. The core of the mountains is composed of a dolomite shale, which outcrops in many places. Especially is the rock near the surface on the steep northwest fault face and where the soil has been removed by the action of glaciers (fig. 16). South of the river the forest on the western slope has been partially destroyed by fire (figs. 16 and 17), but enough of the original stand remains to give a clue to the conditions of the whole slope. A discussion of the burned area will be taken up in another connection.

Wherever the rock outcrops there is little or no vegetation (fig. 16), due to the fact that there is no soil; the pioneer plants on the rocks here, as elsewhere, are the lichens. The crustaceous lichens appear where there is absolutely no disintegrated rock; sometimes associated with these are the foliaceous forms, but these are more common where a little soil has accumulated; with these are found mosses adapted to the dry conditions. After more soil has accumulated, conditions are favorable for plants that require more moisture; among these are the fruitcose lichens, *Cladonia rangiferina sylvatica* being a good example. Associated with these lichens are *Selaginella densa*, *Sedum Douglasii*, *Heuchera parvifolia*, the last being usually found rooted in cracks. These plants prepare the way by their decay for the higher forms that can get a foothold as soon as sufficient soil is present. The inorganic material made by the disintegration of the rocks is blown or washed in from the surrounding region and reinforces the organic accretion. In the meantime the rock crevices have been filling up with soil, thus furnishing favorable places for shrubs like *Prunus demissa*, *Symphoricarpos* sp., *Amelanchier alnifolia*, and *Juniperus sibirica*; and *Campanula rotundifolia*, *Arctostaphylos Uva-ursi*, and grasses are early pioneers in these places. If the outcrop is near a large body of water like Flathead Lake, *Juniperus scopulorum* is one of the first trees. This tree is found distributed around the shores of the lake and along water courses in the prairie region in the valley at the foot of the lake, and with it are found Douglas spruce and bull pine. These of course gain a foothold by sending their roots into the rock crevices and may play an important rôle in the weathering processes by prying the rocks

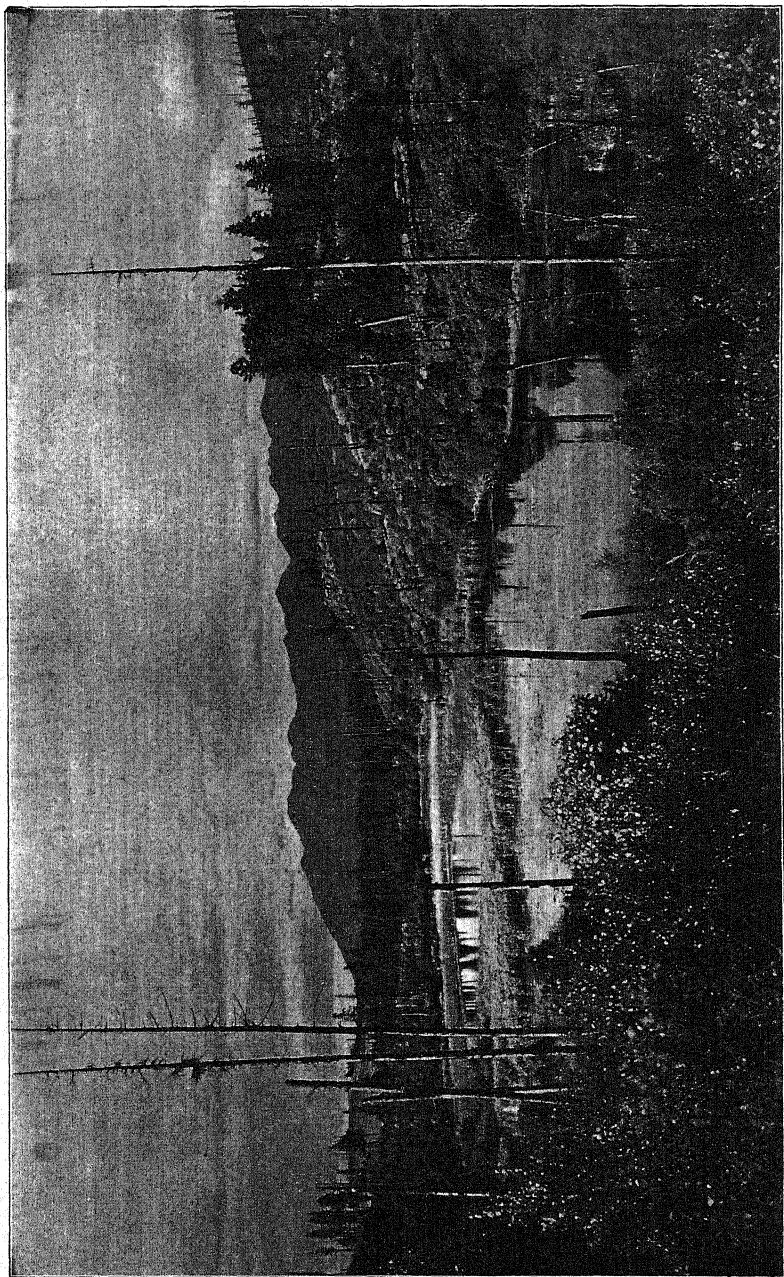


FIG. 17.—View of burned region on west slope of Mission Mountains; Daphnia pond nearly filled with hydrophytic vegetation; the forests of larch, Douglas spruce and bull pine almost entirely destroyed; the bushy growth that becomes vigorous after the forests have been destroyed is *Ceanothus*, *Amelanchier*, *Salix*, etc.—From photograph by ELROD.

apart in the growth of their roots. However, on the rocks there is never more than a scattered growth of trees. Where the soil is less shallow, more trees are present and a more closed stand is developed. In the ravines and other situations where a deep soil has accumulated, a heavy growth often occurs; especially is this true in the protected ravines and on the sheltered slopes. Along the front of Flathead Lake there is a series of ridges which has an open growth of Douglas spruce and bull pine on the side facing the lake; and protected from winds, the slopes on the east side of these ridges and the valley between them and the higher ridges to the east have in addition western larch, which in places is the dominant tree. Again, where the surface of this valley is not far above water level, Engelmann spruce and its associates are found, though these places are infrequent. In many protected areas on the west side of the Mission Range western larch is present, though as contrasted with the eastern slope the exposed western face of the mountains is not so favorable a habitat for the mesophytic trees.

The temperature conditions on top of these mountains and at the foot are not known. No doubt the climate is considerably cooler at an altitude of 1372<sup>m</sup>, the highest point of the range in the plot, than it is at 890<sup>m</sup>, the level of the lake. However, this difference is not enough to exclude the lowland species and introduce those found on the higher Swan Mountains to the east. The presence of a large body of water like Flathead Lake no doubt influences the temperature conditions along its shores, for early fall frosts are less frequent here than at a short distance inland. Whether or not this affects the forest growth is not known.

[*To be concluded.*]

## BRIEFER ARTICLES.

### TERMINOLOGY OF THE SPORE-STRUCTURES IN THE UREDINALES.<sup>1</sup>

SOME time ago I began to study groups of species among the rusts in a more methodical way than usually pursued, and as part of the method undertook to prepare uniform descriptions in which like parts of each structure should receive the same kind of treatment in every case. I soon met with an obstacle that had not been anticipated. The terminology in use was found to be clumsy, ambiguous, poorly correlated, and quite inadequate to show homologies properly.

I will illustrate a few of the difficulties which confronted me. When an aecidium is mentioned, there is a tolerably clear conception of a cup-like structure filled with spores; but when one reaches the next stage of the rust, what is the meaning conveyed by the word *uredo*? I think it is most generally employed as a collective term, referring to the second stage of the rust. We can properly say that the *uredo* occurs on leaves of a certain host, but if we wish to specify a single uredinial structure corresponding to an aecidium, it is necessary to say *uredosorus*; and yet it is not permissible to say *acidiosorus*. Passing to the third stage of the rust there appears to be neither a specific nor a collective name with which to designate it. The nearest approach to a specific term analogous to aecidium is *teleutosorus*, and to a collective term analogous to *uredo* is *teleutostage*. We can say properly that aecidia appeared on a leaf, after a time they were followed by the *uredo*, and finally the teleutospore stage was developed; in which statement we have used three different methods to express the same idea relative to similar spore-structures.

Taking up the first stage again, there appears to be nothing inappropriate in calling the single spore-structure an aecidium so long as we have in mind the first stage of species belonging to the genus *Puccinia* or *Uromyces*; but in the genus *Phragmidium* there is no peridium present, and in *Gymnoconia* not only is the peridium absent but the spore-layer is extended and indefinite, and the term aecidium now seems far less applicable. For such cases it is customary to call the structure a *caeoma*, instead of an

<sup>1</sup> Read before the American Mycological Society at Philadelphia, December 30,



aecidium, adopting the generic name established by TULASNE in 1854, who applied it to forms without a peridium and having the spores in chains. But in the genus *Coleosporium* it is the uredostage, and not the aecidium, that possesses the caeoma structure. Moreover, care must be exercised not to confound TULASNE's caeoma with LINK's caeoma. For in 1809 LINK established a genus *Caeoma* to cover pulverulent forms of rust, whether the spores were borne singly or in chains, which was extensively used by mycologists of the time and subsequently, including SCHWEINITZ and others in America. But the terminology for the first stage of a rust is not yet exhausted. If the stage occurs on a pomaceous host, one is usually safe in calling it a roestelia; and if on a coniferous host, it is usually styled a peridermium. But there are plenty of instances among the less common forms of rust where none of these many terms seems accurate.

Turning to the second stage of rusts fortunately we do not find so many terms in use. The spores are usually borne singly on pedicels, and are generally called uredospores, or when borne in chains they are caeomospores. If the sorus happens to be surrounded or filled with prominent paraphyses, the spores become epiteospores, although this term is derived from a generic name first applied to an aecidial form. It has seemed to me providential that when the uredosorus is surrounded by a peridium, as in species of *Pucciniastrum* and *Cronartium*, we are not required to have some other sort of spore, and are permitted to say simply uredospore.

I have only cursorily mentioned some of the most obtrusive difficulties encountered, when I undertook seriously to record comparative studies of the rusts. I should probably never have publicly rebelled against this confusion of superfluous and yet inadequate terms, had I not after a time become interested in generic nomenclature. So long as there seemed to be no impropriety in allowing a generic name to wear out and be cast aside, or to be subjected to the menial duty of designating a form of spore, it seemed unreasonable to make complaint. But when the conviction became firmly established that a uredineous genus was entitled to as much dignity of position as the genus in any other group of plants; and when it became evident, moreover, that in the application of the rule of priority some of these degraded genera might suddenly assume the place usurped by long accepted names, as for instance, KUNTZE would have us believe that *Roestelia* should take the place of *Gymnosporangium*, then I thought it time to look into the possibility of emending, changing, or in some way improving the terminology of the spore-forms. Pursuing my generic studies further, it appeared little short of absurd that one of the earliest genera, and until recently one of the largest, which has embodied the most

prominent idea of the order both in the scientific mind and in the popular mind, and which supplied the accepted name by which the order is now known, I mean the genus *Uredo*, should be wholly discredited and abandoned, and according to many able mycologists even lose its rights in synonymy. When I came to believe that the names *Uredo*, *Aecidium*, *Roestelia*, *Peridermium*, *Epitea*, and *Caeoma* were entitled to rank as acceptable genera, provided they were not antedated, it became certain that these names should no longer be made to do duty as spore-names.

For the several reasons which I have now partially illustrated, I was impelled to seek for more serviceable, accurate, and concise names for uredineal spore-structures. More than a year ago I presented the first installment of my problem to Dr. FREDERIC E. CLEMENTS, of the University of Nebraska, and it is to his continued and hearty cooperation and suggestion that I am able to present at this time a well considered series of terms to designate the several spore-structures of the Uredinales. I think the claim can be justly made that these new terms, all constructed by Dr. CLEMENTS, will do away with ambiguity, have a definite and easily recognized application, permit of uniformity of statement for the several spore-stages, and promote clear conceptions of homologies.

The terms I have to propose apply to the sorus. By sorus is meant the structure which arises from a single, fertile hyphal mass, or hymenium, either with or without a peridium, now usually called spermogonium, aecidium, uredosorus, teleutosorus, or kindred names. A compound sorus is produced by a number of sori standing close together, separated and surrounded by modified hyphae, which form a stroma, erroneously termed paraphyses, *e. g.*, the teleutosori in *Puccinia rubigovera* and *Puccinia Virgaureae*. The stroma is not considered a part of the sorus, but an adjunct structure. A simple sorus is surrounded by the tissues of the host, or by unmodified mycelium, and includes the peridium, and all true paraphyses, whether peripheral or discal.

The new terms consist of four words, with their derivatives, one for each of the four stages of uredineal fungi. For the sorus of the initial stage, usually designated by a cipher, and called spermogonium, pycnidium, etc., I propose *pycnium* (πυκνίον); derivatives *pycnial*, *pycniospores*, etc. For the sorus of the first spore-stage, usually designated by the Roman numeral I, and called aecidium, roestelia, peridermium, etc., I propose *aecium* (αἰκίον); derivatives *aecial*, *aeciospore*, etc. For the sorus of the second spore-stage, usually designated by the Roman numeral II, and called uredosorus, etc., I propose *uredinium* (uredo); derivatives *uredinial*, *urediniospore* or if preferred *uredospore*, etc. For the sorus of



the third spore-stage, usually designated by the Roman numeral III, and called teleutosorus, I propose *telium* (τέλιον); derivatives *telial*, *teliospore*, etc.

These four words and their derivatives have sufficient resemblance to corresponding terms now in use to suggest their meaning, and thus facilitate their introduction; and yet they are all new words and are now brought before the scientific public for the first time. All the words are shorter than the corresponding ones now in use, except urediniospore, which is longer by three letters than uredospore, but no more difficult to pronounce, and for this the word at present in use, uredospore, may well be retained. No permissible shortening of the stem of this term has seemed feasible, and yet have the uniformity and classicism of the series preserved.

I may be permitted to illustrate the use of these words by a similar sentence to that employed at the beginning of my paper. In the case of wheat rust, aecia appear on the leaves of the barberry in spring, preceded by pycnia; the aeciospores give rise in due course of time to uredinia on the wheat plant, followed by telia. A similar statement could be made for a Coleosporium, Phragmidium, or any other rust. One might explain the difference between the telial stage and the uredinial, or discuss the status of pycniospores as compared with teliospores or other sorts, or he might point out that the sorus of a uredinium has the same essential structure whether without peridium and stylosporid, as in Puccinia; with peridium and stylosporid, as in Pucciniastrum, or without peridium and the spores in chains, as in Coleosporium; and so on.

Finally, the acceptance of these terms would require that the following terminology for the receptacles, spores, etc., of the rusts should be substituted for the series recently given by SACCARDO in his *Nomenclatura mycologica*, viz., sorus, pycnium, aecium, uredinium, telium, peridium, stroma. Mesospore, amphispore, stylospore, etc., are special descriptive terms, which may be extended indefinitely as need arises, but do not form part of the general category. Caeomospore, epiteospore, aecidiospore, and other terms compounded from generic names should be wholly discontinued. Peridium is to be preferred to pseudoperidium, in accord with the usage of DECANDOLLE, LÉVEILLÉ, and many recent mycologists. Brevity, directness, and accuracy are excellent qualities to keep in mind when deciding upon terminology.—J. C. ARTHUR.

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# CURRENT LITERATURE.

## BOOK REVIEWS.

### Plant chemistry.

MANY BOOKS have been written on physiological chemistry, but for the most part these deal specifically with substances which are of chief interest to the animal physiologist; and generally they undertake to treat the characteristics and modes of reaction of a very great number of individual substances more or less independently of their biological relations. The book before us has a definite aim. CZAPEK<sup>1</sup> has sought to bring together a collection of facts which should be at once complete and critically verified, in order that these may form a point of departure for further researches. The field of plant chemistry has been so neglected, comparatively, that scarcely more than ordinary industry suffices to make notable advances in knowledge.

Such a book, of course, will be of value to many other than plant physiologists. The service which CZAPEK has done is likely, therefore, to have wide and hearty appreciation. The book is not intended for the beginner in biochemistry, but assumes a general knowledge of both botany and chemistry, being intended specifically as a reference book and repertory of literature for the help of investigators of special problems.

The book opens with a brief historical introduction, in which the author touches lightly yet clearly the service of chemists of the Middle Ages and of those who labored after the transformation which chemistry underwent through the genius of LAVOISIER. The work then is divided into two parts, general and special. The general part occupies something over ninety pages, and is of decided interest to the reader who is familiar enough with modern chemistry to appreciate this brief and illuminating discussion. The author considers the nature of the protoplasm and the substances of which it is composed; the properties of colloids, the structure of the protoplasm and its biochemical significance; the conditions and rate of chemical reactions, and especially the ionic reactions in living cells. The last three sections, in which are discussed catalysis and catalysers, the general chemistry of enzymes, and the cytotoxines and similar compounds, deserve particular notice.

The special part of the present volume is confined to a consideration of fats, lecithines, phytosterines, waxes, and the carbohydrates. To the last named much the larger part of the volume is devoted. Each of these classes of materials is discussed in its relations to various groups of plants, or to the various plant parts in which it is found. In this feature we have the most radical difference between

<sup>1</sup> CZAPEK, F., *Biochemie der Pflanzen*. Bd. I. Imp. 8vo. pp. xv+584. Jena: Gustav Fischer. 1904. M 14.

this book and most of the previous works on physiological chemistry, and even of the few that have been written with special reference to plant chemics.

A second volume is already in press and may be expected ere long. We suppose that a detailed treatment of the proteids will occupy the greater part of it. It will be accompanied by full indexes.—C. R. B.

#### Plant organization.

IN 1899 we noticed the first part of a work by BERTHOLD on plant organization,<sup>2</sup> of which the first half of the second part, promised "very soon," has recently appeared.<sup>3</sup> The author announced his intention of discussing in this second part in a comprehensive way the investigations made by himself and others. This promise rests in large part unfulfilled.

We find an "introduction" of twenty-one pages (which seems queerly out of place in the middle of a book) setting forth the aims and methods of this "Physiologie der pflanzlichen Gestaltung." BERTHOLD assumes that the protoplast is a mechanism, made of different individual parts, even though they cannot be distinguished, each having its particular function. This assumption is developed at length. Of course, therefore, he objects to the idea of adaptation in connection with anatomy, especially as developed by HABERLANDT. He rejects the ideas of growth enzymes and of *Anlagen* as indicating useful directions for research, and minimizes the value of studies on regeneration in the problem of plant organization.

In the special part (pp. 22-257) BERTHOLD discusses in four chapters the morphology of the typical (*sic*) shoot, the pith, the primary cortex, the course of development in the pith and cortex, and entitles the fifth "a comprehensive synopsis of the development and rhythm of the shoot." These chapters make almost no reference to the "mechanism" on which he lays so much stress in the introduction, and certainly do nothing toward revealing it. Profuse details encumber the pages; indeed, in places it almost seems as though the author had published his notebook. The "synopsis" covers 136 pages, a formidable number for a "glance" to take in. It is so beclouded with details and so unorganized that one cannot readily discover what the author is driving at. Great stress is laid throughout upon the cell-contents as determining factors in the final configuration of tissues, yet there is no indication of the nature of the relation, and such categories as "starch," "sugar," and "tannin" are treated as though they were definite substances. It is quite certain that the author has not yet succeeded in picturing clearly either the anatomical or physiological features of plant organization. Perhaps the next instalment will sum up his views in a definite and precise fashion.—C. R. B.

<sup>2</sup> BOT. GAZ. 27:146. 1899.

<sup>3</sup> BERTHOLD, G., Untersuchungen zur Physiologie der pflanzlichen Organisation. 8vo. pp. iv + 257. Leipzig; Wilhelm Engelmann. 1904.

## MINOR NOTICES.

THE TENTH AND ELEVENTH parts of ROTH's<sup>4</sup> *Die europäischen Laubmoose* complete the second volume and the work. Supplements to both volumes and indexes to accepted names and synonyms in the second volume make up the larger portion of the eleventh part. The four indexes (two in the first volume) should have been combined into one for convenience, though we are thankful for full indexing of any kind. The author and publisher deserve special commendation for the promptness with which the work has been issued. The book will be almost as useful to American as to European bryologists, and the total price, 44 marks, for a work with 62 plates and nearly 1400 pages is certainly very reasonable.—C. R. B.

MAJOR SQUIER,<sup>5</sup> of the Signal Corps, U. S. A., in experimenting with field wireless telegraphy, has incidentally paid some attention to the conductivity and electromotive force of live trees. Being, naturally enough, unfamiliar with the literature, he has rediscovered a number of well-known phenomena and raises some questions which have already been investigated. The discharge of a powerful induction coil and Leyden jars through live-plant electrodes, and the so-called "floral spectra" with lines of carbon, nitrogen, sodium, etc., are more novel than valuable.—C. R. B.

*Die Pflanzenfamilien* drags on, the sections on mosses and lichens not yet being complete. The former are being elaborated by BRÖTHERUS.<sup>6</sup> The last two parts to appear (219, 220) treat the remainder of the Bryaceae, the monotypic Leptostomaceae, Mniaceae (72 spp.), Rhizogoniaceae (35 spp.), Aulacomniaceae (11 spp.), Meesiaceae (11 spp.), Catosciopaceae (monotypic), Bartramiaceae (400 spp.), Timmiaceae (10 spp.), Weberaceae (13 spp.), Buxbaumiaceae (2 spp.), Calomniaceae (3 spp.), and Georgiaceae (5 spp.). The Polytrichaceae are just begun.—C. R. B.

BEAL<sup>7</sup> has published what is really a third edition of the list of vascular plants that bears the title "Michigan Flora." The first edition (1880) was prepared by C. F. WHEELER and ERWIN F. SMITH; the second (1892) by C. F. WHEELER and W. J. BEAL; and this third edition bears only the name of Professor BEAL. Besides the incorporation of additional plants, the most notable

<sup>4</sup> ROTH, G., *Die europäischen Laubmoose*. 2 Band, Lief. 10, 11. Imp. 8vo. pp. 573-734. pls. 41-62. Leipzig: Wilhelm Engelmann. 1904. Each M 4. Parts not sold singly.

<sup>5</sup> SQUIER, GEORGE O., On the absorption of electromagnetic waves by living vegetable organisms. 8vo. pp. 32. Reprinted from Maj. Gen. Arthur MacArthur's Report to War Dept. on Military Maneuvers in the Pacific Division, 1904.

<sup>6</sup> ENGLER and PRANTL, *Die natürlichen Pflanzenfamilien*. Lief. 219, 220. pp. 577-672. figs. 264 in 37. Leipzig: Wilhelm Engelmann. 1904. M 6 or 12.

<sup>7</sup> BEAL, W. J., *Michigan Flora*. A list of the fern and seed plants growing without cultivation. Reprinted from 5th Report of the Mich. Acad. Sci. 1904.

change in the present edition is the use of the Engler and Prantl sequence as presented in Britton's *Manual*.—J. M. C.

THE SECOND FASCICLE of LÉVEILLÉ's<sup>8</sup> monograph of *Oenothera* has appeared, the first fascicle having been noticed in this journal for April 1903 (p. 296). Naturally it is of great interest to American taxonomists, and contains a profusion of illustrations. The genera *Eulobus* and *Gayophytum* have been merged under *Oenothera*, and *O. bistorta* Nutt. has been replaced in great part by *O. chieranthifolia* Hornem.—J. M. C.

THE FOREST WEALTH OF OREGON is the title of a small pamphlet prepared by E. P. SHELDON<sup>9</sup> setting forth the forest resources of the state, with a list of forest trees and larger shrubs. Of these thirty-eight are gymnosperms.—C. R. B.

IN CONTINUING his revision of *Eucalyptus*, MAIDEN<sup>10</sup> presents *E. stellulata*, *E. coriacea*, and *E. coccifera*, under each species giving the description, synonyms, range, and affinity.—J. M. C.

THE EIGHTH VOLUME of the fourth series of HOOKER's *Icones Plantarum* closes with the publication of the fourth part January 1905. The plates of this part are 2776–2800.—J. M. C.

#### NOTES FOR STUDENTS.

HESSelman<sup>11</sup> has published a paper on Swedish meadows, which should be carefully read by all who are engaged in ecological research, since no recent paper has gone more fundamentally or successfully into the real problems of ecology. The studies have been carried on for nearly a decade, and in a rather limited area in the neighborhood of Stockholm, and with especial detail on the little island of Skabbsholmen. The "Laubwiesen" are meadows in which there are scattered deciduous trees, the general aspect being park-like. They might perhaps be regarded as edaphic savannas. These formations are rich in herbs and grasses, and are essentially without low shrubs. At an earlier time the "Laubwiesen" covered extensive areas, but they are now restricted to what may be called new terranes, especially near the coast and about inland lakes. They seem to be particularly favored by maritime climates and calcareous soils. Floristically the vegetation is closely related to that of oak or beech woods on calcareous soil rich in humus. The dominant trees are ash, oak, linden, elm, and beech,

<sup>8</sup> LÉVEILLÉ, H., Monographie du genre *Oenothera*. Le Mans. 1905. 100 fr.

<sup>9</sup> SHELDON, E. P., The forest wealth of Oregon. 12mo. pp. 32. pls. 4. Portland, Ore. Printed by direction of the Lewis and Clark Exposition Commission. 1904.

<sup>10</sup> MAIDEN, J. H., A critical revision of the genus *Eucalyptus*. Part V. pls. 4. Published by the authority of the Government of the State of New South Wales. 1904. 2s. 6d.

<sup>11</sup> HESSELMAN, H., Zur Kenntnis des Pflanzenlebens schwedischer Laubwiesen. Eine physiologisch-biologische und pflanzengeographische Studie. Beih. Bot. Cent. 17:311–460. pls. 4–8. 1904.

while the hazel is the chief shrub. The herbage is so dense as to exclude most mosses. The formation is often developed from salt marshes and HESSELMAN gives an interesting account of the developmental stages. The alder is commonly the pioneer ligneous form, and is followed by the ash. The author's most important contribution is experimental, and in this field he has clearly pushed forward the frontiers of our knowledge. His results deal chiefly with the ecology of starch formation, respiration, and transpiration. An important feature of his results is that they are rigidly quantitative. In the study of starch formation, close correlation was made with the light intensity, in which WIESNER's methods were employed. The "Lichtgenuss" varied from about 1 in open meadows to  $\frac{1}{16}$  in dense hazel thickets. Much formation of starch was observed under the trees in early spring, and all through the summer as well in open meadows. The very same species that were found rich in starch in the woods in spring were found nearly without it in the summer shade. In the ash woods, however, starch is formed in summer by all herbs, except a few which are always poor in starch. This is correlated with the greater light intensity of ash woods, as compared with other kinds. Anatomical studies are also correlated with the above, and it is found that those plants which develop their leaves late in the forest shade have a weak development of palisade cells, while the plants which develop their leaves in the intenser light of early spring have more palisades. Trees with high light requirement were found to have but one leaf type, namely a sun leaf; while shade-enduring trees have both sun or shade leaves, depending on their growth conditions. Trees of the first class, such as the ash or birch, show starch formation in all leaves, wherever placed. Plants of the second type, such as oak or hazel, do not form starch in the innermost leaves. In equal light shade leaves form more starch than do sun leaves of the same species. Starch formation decreases from spring to summer in the woods more in sun plants than in shade plants. Shade plants respire much less than do sun plants. Shade plants transpire much less in the shade than do sun plants in the sun, especially on hot or dry days. The leaf surface being equal, plants transpire more as they have a greater development of palisade cells, though many have thought that palisade cells in some way check transpiration, since they commonly occur where such protection seems necessary.

The great detail with which HESSELMAN's studies have been pursued, and the tedious quantitative experiments, may well furnish a model for many workers in all lands. The paper is illustrated by several reproductions of photographs, and a number of text figures showing anatomical details.—H. C. COWLES.

THE ACHROMATIC figure in *Pellia epiphylla* has been investigated again, this time by GREGOIRE and BERGHS,<sup>12</sup> who have devoted their attention to the intrasporal mitoses of the germinating spore, and in some degree to the first mitosis in the spore mother-cell. The figures show some improvement over those of their predecessors and indicate a technique of the highest order. The researches of

<sup>12</sup> GREGOIRE, V., and BERGHS, J., La figure achromatique dans le *Pellia epiphylla*. La Cellule 21: 193-233. pls. 1-2. 1904.

DAVIS and of the reviewer are frequently discussed through the work. In the opinion of the reviewer, our technique was also good and enabled us to see the structures described in the present paper, so that differences in conclusions are due in large measure to differences in interpretation of structures which other investigators have seen. The present writers support the reviewer's conclusions that the two poles of the chromatic figure arise in succession and independently, and also that the nuclear membrane belongs to the category of the *Hautschicht*. Without details, some of the principal conclusions are the following: In the segmentation of the spore (beginning with the third mitosis) the asters are continuous from pole to pole and the achromatic figure surrounds both the nucleus and the "polar vesicles" ("caps"). The achromatic figure results simply from a rearrangement of the general cytoplasmic reticulum. Neither the nucleus nor the vesicles (caps) contribute to the formation of the spindle. The vesicles are nothing but nuclear sap diffused into the cytoplasm. After mitosis the achromatic structures are transformed into the general cytoplasm of the cell. At no stage is there a genuine centrosphere or centrosome. The first mitoses in the germinating spore and the mitoses in the spore mother-cell show neither asters nor polar vesicles (caps), but in other respects the evolution of the achromatic figure is the same as in other mitoses. The authors hold that there is no distinction between kinoplasm and trophoplasm. No importance is attached to the structure described by others as a centrosphere. These researches on *Pellia* contradict many theories in regard to the mechanism of mitosis.—C. J. CHAMBERLAIN.

PHILLIPS<sup>13</sup> has contributed some startling discoveries to an already confused subject. Particularly interesting are his conclusions as to the structure of the central body of the Cyanophyceae, which he regards as a nucleus, and the occurrence of sexual fusions in the formation of the spores. In unsectioned filaments, since "sections revealed very little that could not be seen equally as well in the uncut object," the author has discovered that the chromatin of the central body is aggregated in hollow vesicles in the resting cell. This vesicular appearance disappears in the dividing cell and the chromatin granules become arranged in a loose network. In this condition, he finds the minute granules themselves multiplying by transverse division. Nuclear division follows, which may be by one of two modes, both occurring even in the same species. One, according to the author, evidently corresponds to a direct division, while the other is a primitive mode of karyokinesis. The latter resembles closely the method of mitosis described by KOHL,<sup>14</sup> in which a double transverse division occurs in the spirem thread, never a longitudinal splitting. The author has also discovered thick-walled spores in *Oscillatoria*, which are produced after the fusion of several cells

<sup>13</sup> PHILLIPS, O. P., A comparative study of the cytology and movements of Cyanophyceae. Contrib. Bot. Lab. Univ. Pennsylvania 2:237-335. pls. 23-25. 1904.

<sup>14</sup> KOHL, F. G., Ueber die Organisation und Physiologie der Cyanophyceenzelle und die mitotische Theilung ihres Kernes.

(one to four) into one, and after certain adjoining cells, called by him "nurse cells," have gradually disintegrated and given up their chromatin to the forming spore. The first fusion is regarded as probably a sexual act, but he does not appear to attach this importance to the giving up of the chromatin by the "nurse cell." His figures of the spores of *Oscillatoria* remind one of small hormogonia, while his "nurse cells" evidently correspond to the cells adjacent to the hormogonia which have been heretofore regarded as collapsed, dead cells.

The author makes a third distinct contribution, which is also far from convincing, in that he finds that the movements of the Cyanophyceae are caused by delicate cilia, distributed along the sides of the filament.—EDGAR W. OLIVE.

THE OVULE of seven genera of cycads, *Zamia*, *Macrozamia*, *Ceratozamia*, *Encephalartos*, *Bowenia*, and *Dioon*, have been investigated by Miss STOPES.<sup>15</sup> The work was done in GOEBEL's laboratory and the standpoint is that of phylogenetic anatomy.

The integument in all the forms studied is differentiated into three layers, the outer and inner being fleshy, while the middle is the well-known stony layer. The inner system of bundles does not lie in the nucellus (which in all living cycads and their fossil relatives is absolutely without vascular bundles), or between the nucellus and integument, as is commonly supposed, but belongs to the inner fleshy layer of the integument. These bundles, which in all the seeds examined are similar and simple, sometimes extend beyond the nucellus, reaching almost to the micropyle. The larger ones are collateral and the phloem is not strongly developed. It is often hard to determine where the protoxylem lies, but, in general, the bundles are endarch. In the simplest case, these bundles come from the branching of a single concentric or nearly concentric bundle.

The bundles in the outer flesh, with few exceptions, are collateral, with outer phloem and inner mesarch xylem. The central strand, from which these bundles come, is usually concentric.

It is certain that the fossil seed, *Lagenostoma*, is related to living cycads. Evidence indicating this relationship is presented in detail and is illustrated by diagrams. Miss STOPES believes that *Lagenostoma* lies near the common origin of the two groups. The single integument of the cycads is thought to correspond to the two separate integuments of *Lagenostoma*.

It is particularly interesting to note that *Cycas* itself, generally thought to be the most primitive of the cycads, has the most highly developed seed to be found in the group.—C. J. CHAMBERLAIN.

ZACHARIAS<sup>16</sup> adds another article to his long series of writings on the structure of the cyanophyceous cell, which leaves the subject in deeper uncertainty than ever. This latest addition is in the main a sharp criticism of the methods and

<sup>15</sup> STOPES, MARIE C., Beiträge zur Kenntniss der Fortpflanzungsorgane der Cycadeen. *Flora* 93:435-482. figs. 37. 1904.

<sup>16</sup> ZACHARIAS, E., Ueber die Cyanophyceen. *Jahrb. Hamburg Wiss. Anat.* 21:49-89. *pl. I.* 1903.



conclusions of KOHL and a reiteration of the principal results of his paper of 1890. He thinks that KOHL's "chromatin granules" were probably his small "Zentralkörner," or slime globules. While ZACHARIAS denies that it has been proved that the central body contains any granules other than the "Zentralkörner," yet he leaves the question still open as to the possibility of the existence of chromatin in this enigmatical body. He asserts strongly his belief, however, after an examination of the preparations of both KOHL and HEGLER, that there are no structures present which can be called chromosomes, as maintained by KOHL and BÜTSCHLI.

ZACHARIAS adds in the present paper some new observations on the nature of the cyanophycin granules. After repeating his earlier experiments on the effects of dilute HCl, he comes to a conclusion somewhat at variance with his earlier results, namely, that the granules in certain cases are not actually dissolved by the acid, but that nevertheless they undergo some change. He concludes, further, that there is no difference in the behavior of the cyanophycin toward dilute HCl and toward pepsin, thus disputing the results of HEGLER and KOHL. The author as well cannot agree with these investigators in their conclusions as to the albuminous and crystalloidal nature of the cyanophycin granules, although he adds nothing in support of his earlier supposition of their carbohydrate nature.

In regard to the duration of cyanophycin in filaments grown for a long time in the dark, ZACHARIAS differs from HEGLER and KOHL in asserting that there is no complete disappearance of cyanophycin and slime.—EDGAR W. OLIVE.

KOERNICKE reviews critically the present condition of researches upon the plant cell,<sup>17</sup> confining his attention to the morphological aspect now commonly spoken of as cytology. A little more than one half the work is devoted to the cytoplasm, the rest dealing with the nucleus.

That modern preparations do not show a series of artifacts but give a reliable view of structures, is proved by observations upon living material. The cytoplasm is regarded as consisting of two distinct substances, the kinoplasm and the trophoplasm. Spindle formation is described in all groups and the various views are clearly presented. The centrosome problem is discussed at some length. An impartial summary of the literature dealing with the blepharoplast is given, but the author expresses no opinion as to its homology. The nuclear membrane, cell plate, and *Hautschicht* are regarded as kinoplasmic structures. The paragraphs on protoplasmic continuity are especially valuable because the important investigations are so recent. Less attention is paid to the cell wall.

In treating the nucleus, the author deals principally with the works which have appeared since 1896, the date of Zimmerman's book on the nucleus, since when many investigators have studied the nuclei of the lower plants, especially the schizophytes and yeasts. Of course, the discussion of the chromatin occupies most of the space devoted to the nucleus. It is rather surprising that the Chara-

<sup>17</sup> KOERNICKE, M., Der heutige Stand der pflanzlichen Zellforschung. Ber. Deutsch. Bot. Gesells. 21: Generalsammlungs-Heft 66-134. 1904.

ceae, Liliaceae, and Amaryllidaceae should be credited with the largest nuclei, for their nuclei are small when compared with those of the eggs of some gymnosperms.

No figures are given, but the references are very numerous and authority is cited for every statement.—C. J. CHAMBERLAIN.

AFTER REVIEWING several of the more important publications regarding the statolith theory, TISCHLER<sup>18</sup> states that adequate evidence to establish a correlation between movable starch grains and the perception of the gravitation stimulus is not available; and it is his opinion that such evidence cannot, with present methods, become available, for the simple reason that while the reaction may be optically observed the perception is hidden and a constancy of quantitative relation between the two cannot be depended upon. For similar reasons, the author believes a demonstration of the statolith theory cannot come from the study of organs which are little or not at all reactive; hence we must regard his contribution as consisting of merely circumstantial evidence. The general trend of the paper is that in the various types of roots slightly or not at all geotropic, geotropism and starch migration are coincident and associated phenomena. He finds that in adventitious roots which are constantly ageotropic these starch grains are either not present in the cap or if present are irregularly distributed. In temporarily ageotropic roots the starch grains are either absent or if present are irregularly distributed during the ageotropic period. With incipient geotropism, however, the starch grains appear if previously absent, and commence to collect and function as statoliths. When geotropic response is prevented by the application of stronger stimuli, the starch grains which would otherwise change position to function as statoliths do not do so. Some of the orchids having aerial roots slightly geotropic do not have starch grains, and the author calls in chloroplasts of the root-cap to act as statoliths.—RAYMOND H. POND.

PALEOBOTANICAL NOTES.—STENZEL<sup>19</sup> has just published a very elaborate and valuable monograph describing all the known forms of fossil palm-wood.—NATHORST<sup>20</sup> briefly summarizes our knowledge of Antarctic fossil floras. A rather rich deposit of Jurassic age on Louis-Philippe Land yields numerous remains of *Cladophlebis*, besides representatives of *Brachyphyllum*, *Elatides*, *Palissya*, *Taxites*, *Araucarites*, *Otozamites*, *Pterophyllum*, *Equisetum*, *Sagenopteris*, *Thinnfeldia*, *Scleropteris*, and *Stachypteris*; all characteristic Jurassic forms, emphasizing the uniform cosmopolitan character of the Jurassic flora even in lat. 63° 30' S. Seymour Island in lat. 64° S. yields fragments of a dicotyledon, of *Araucarites*, and of a conifer resembling *Sequoia*. The Malouine Islands furnish

<sup>18</sup> TISCHLER, G., Ueber das Vorkommen von statolithen bei wenig oder gar nicht geotropischen Wurzeln. *Flora* 94: 1-68. figs. 31. 1905.

<sup>19</sup> STENZEL, K. G., Fossile Palmenhölzer. *Beitr. Palaeont. u. Geol. Oesterr. Ungarn. fol. pp.* 182. pls. 22. 1904.

<sup>20</sup> NATHORST, A. G., *Compt. Rend.* 138: 1447-1450. 1904.

fragments of an *Asterocalamites* indicative of Upper Devonian or Lower Carboniferous age.—MAURY<sup>21</sup> reports *Hicoria minor*, *Castanea vulgaris*, *Fagus phiocenica*, *Ilex aquifolium*, and *Bambusa lugdunensis* from a new Pliocene locality at Capelle in the Department of Cantal, south central France.—HARTZ<sup>22</sup> records characteristic spikes of the common *Dulichium arundinaceum* (L.) Britt. of eastern North America, along with the remains of *Picea*, *Brasenia*, *Hydrocharis*, *Carpinus*, and *Betula*, from the interglacial of Brörup in southern Jutland, Denmark.—EDWARD W. BERRY.

HUME<sup>23</sup> calls attention to the anthracnose of the pomelo in Florida caused by *Colletotrichum gloeosporoides*. He reported in 1900 an injury to pomelo leaves caused by this fungus, a disease that was then referred to as leaf spot. HUME first noticed the same fungus on pomelo fruits in 1901 and now reports it upon twigs of the same plant. It is also known to cause a disease of lemon and lime fruits and is frequently seen on the leaves and twigs of the sweet orange and rarely on its fruit. Trees whose vitality has been reduced by improper soil conditions or by mechanical injury or through injuries inflicted by winds, frost, insects, or other diseases are more subject to this anthracnose than trees in perfect condition. It is recommended that all diseased fruits and branches be removed and burned and the trees sprayed with the usual Bordeaux mixture early in the season from May to July. Spray treatment should particularly be applied to trees whose branches show any evidence of the anthracnose. It is also recommended that the fruit be washed, before packing, with water to which has been added some ammoniacal copper carbonate solution or potassium sulfid. The later treatment will prevent the serious injury to the fruit that frequently occurs on the way to market.—E. MEAD WILCOX.

BY MEASURING the distance between oppositely located branches of small trees and shrubs, GANONG<sup>24</sup> has established that with autumnal defoliation the branches commence an inward movement toward the main axis. This inward movement continues after defoliation, reaching a limit with the full winter condition in January. With the swelling of the buds in April a reverse movement commences which continues through vernal foliation to the full summer condition in June. The movement accompanying defoliation and foliation is attributed merely to decreasing and increasing weight of branches, by loss and gain of leaves, but the intervening movement is regarded as indirectly thermometric because from experimental data (quite limited and so regarded by the author) it seems that the movement is correlated with variations in the amount of water in the stem and

<sup>21</sup> MAURY, P., *Le Monde des Plantes*, Nov. 1903, pp. 54-55.

<sup>22</sup> HARTZ, N., *Meddel. Dansk. Geol. Foren.* 10:13-22. *figs.* 5. 1904.

<sup>23</sup> HUME, H. HAROLD, Anthracnose of the pomelo. *Bull. Florida Exp. Stat.* 74:157-172. *pl.* 1-4. 1904.

<sup>24</sup> GANONG, W. F., An undescribed thermometric movement of the branches in shrubs and trees. *Ann. Botany* 18:631-644. *figs.* 6. 1904.

that fluctuations in temperature induce such variations in water content. The author regards the movement as without ecological significance. The practical absence of other literature on this subject gives the paper a quality of uniqueness, and although negative results appear to equal the positive in number, the high ideals of the accurate and unprejudiced worker are everywhere suggested.—RAYMOND H. POND.

GANONG has published in an earlier paper his<sup>25</sup> views concerning some of the underlying principles of ecology, and to these he has added others<sup>26</sup> dealing especially with adaptation. After criticising the idea that ecology is synonymous with ecological geography, and deploring the lack of any significant advance in ecological methods in recent years, he plunges into a discussion of the philosophy of adaptation. Five principles are laid down; the first, as to the reality of adaptation, and the last, as to the inevitable imperfection of all adaptation, must meet with general acceptance. The second principle, dealing with the evolutionary phylogeny of adaptation, is taken up from a Lamarckian standpoint. GANONG thinks that the concomitance of diverse adaptations in a single species is to be accounted for best along Lamarckian lines. While this is doubtless true, there are as many objections to the Lamarckian as to other theories; indeed, some authors (DETTO<sup>27</sup> for example) regard the Lamarckian theory as the most untenable of all. The third and fourth principles are concerned with adaptation as a race process rather than an individual process, and with the metamorphic nature of its origin.—H. C. COWLES.

TANSLEY'S<sup>28</sup> address before the British Association on *The problems of ecology* is very suggestive, and indicates the rapid progress which is being made along ecological lines in the British Isles. TANSLEY proposes to narrow the definition of ecology to include only its geographic aspects. For instance, he would include the geographic distribution of pollination mechanisms, but would exclude the study of pollination mechanisms themselves. The reviewer can well imagine what a shock this will give to those who imagine that ecology includes nothing but the study of seed dispersal and pollination! TANSLEY uses as a synonym of ecology topographical physiology, which is practically identical with what the reviewer has termed physiographic ecology. It does not seem likely that TANSLEY'S view as to the limits of ecology will meet general approval, since the broader term has been so universally regarded as highly desirable and much needed. The distinctions between descriptive and experimental ecology are well brought out, and proper emphasis is laid upon the ultimate aim of ecology, the discovery of causes.—H. C. COWLES.

<sup>25</sup> See BOT. GAZ. 36:447-453. 1903.

<sup>26</sup> GANONG, W. F., The cardinal principles of ecology. Science 19:493-498. 1904.

<sup>27</sup> See BOT. GAZ. 38:385-386. 1904.

<sup>28</sup> TANSLEY, A. G., The problems of ecology. New Phytologist 3:191-200. 1904.

PARTHENOGENESIS in *Taraxacum* and *Hieracium* is being investigated by MURBECK.<sup>29</sup> Two species of *Taraxacum* were studied, *T. vulgare* (Lam.) Raunk., which produces abundant, but imperfect pollen, and *T. speciosum* Raunk., which produces no pollen at all. The embryo-sacs present nothing unusual in their appearance. The egg cell increases in size, its nucleus divides, and the embryo is formed just as if normal fertilization had occurred. The polar nuclei fuse and then divide, giving rise to the endosperm.

Three species of *Hieracium* were examined, *H. grandidens* Dahlst., *H. serratifrons* Almqu., and *H. colophyllum leiopogon* Gren. In general, the embryo-sac resembles that of *Taraxacum*. The embryo is developed from the egg, and embryos are formed in eighty per cent. or ninety per cent. of the flowers, so that it is probable that these species are always parthenogenetic. A full account with illustrations is to follow.—C. J. CHAMBERLAIN.

MISS COOLEY<sup>30</sup> has given an account of the ecology of the tamarack, which has been based upon a considerable amount of field study in various states. Attention is called to the unusually wide range of the tree, which occurs in five of MERRIAM'S zones. The tree displays great vigor even at the extreme northern and southern limits. The range of topographic habitat is also wide; although commonly thought of as a swamp tree, it occurs in almost every habitat, even to the most xerophytic. Among the characteristics which may serve to give this tree its great success, Miss COOLEY mentions the abundance of seeds, the frequency with which the tree produces seeds, the power of the seedlings to endure light, indifference to soil, and rapid growth. A great disadvantage is the inability of the tree to endure shade, or to compete with other forest trees. In a Maine area a tamarack swamp<sup>3</sup> has succeeded a hardwood forest.—H. C. COWLES.

APOGAMY in *Hieracium* is described by OSTENFELD,<sup>31</sup> who in 1903 in a paper written conjointly with RAUNKIAER reported that twenty-two species of the genus had been found to produce seeds even after pollination had been prevented. OSTENFELD now finds that many of the seeds thus produced germinate normally. In the botanical garden at Copenhagen two species of *Hieracium* were found which produce only female flowers, a careful examination showing not a single pollen grain. These plants were isolated under control in the greenhouse and produced abundant seeds. Whether the embryos arise from unfertilized eggs was not determined. Attempts to germinate the pollen of pollen-bearing species failed. This would indicate that the great number of forms in the genus, usually attributed to hybridization, are due rather to mutation. All attempts to produce hybrids were unsuccessful.—C. J. CHAMBERLAIN.

<sup>29</sup> MURBECK, Sv., Parthenogenese bei den Gattungen *Taraxacum* und *Hieracium*. Bot. Notiser 1904:285-296.

<sup>30</sup> COOLEY, GRACE E., Silvicultural features of *Larix americana*. Forestry Quarterly 2:148-160. 1904.

<sup>31</sup> OSTENFELD, C. H., Zur Kenntniss der Apogamie in der Gattung *Hieracium*. Ber. Deutsch. Bot. Gesells. 22:376-381. 1904.

THE NUTRITION of the chromatin thread and the chromosomes by nucleolar material is well shown, according to VON DERSHAU,<sup>32</sup> in the active nuclei of the parietal endosperm of *Fritillaria imperialis*. The increasing staining capacity of the chromatin thread is correlated with the dissolution of the nucleoli; besides, slender connections unite the nucleoli and the thread and indicate a streaming of material. Resting nucleoli are spherical or ellipsoidal, while those in the active condition are more or less irregular or star-shaped. A study of karyokinesis showed a direct relation between the nucleoli and spindle formation. An investigation of the development of the peristome of *Funaria hygrometrica* and *Bryum argenteum* showed that the nucleoli play an active part in the local thickenings of the cell wall. VON DERSHAU draws the conclusion that the nucleoli consist of reserve substance.—C. J. CHAMBERLAIN.

BISPORANGIATE STROBILI have not hitherto been observed in *Juniperus*, and only a single case has been reported for the Cupressineae. An interesting case is described by RENNER<sup>33</sup>, who discovered a plant which bears such strobili almost exclusively. Only on a few twigs, and here only toward the tips, was there a transition to purely ovulate strobili. In the base of the bisporangiate strobilus there are a few sterile leaves, above these are two or three whorls of staminate sporophylls, and at the tip are the ovules. There may be a whorl of sterile leaves between the staminate sporophylls and the ovules. The pollen develops normally, but so much later than the ovules that there is no possibility of self-pollination. RENNER sees in these bisporangiate strobili a suggestion of the method by which the bisporangiate flowers of angiosperms may have arisen.—C. J. CHAMBERLAIN.

WHITE<sup>34</sup> has published the first American contribution to our knowledge of those paleozoic fern-like plants which had acquired the seed-habit, a subject under active investigation abroad of late. He records abundant gymnospermous fruits in the fern-genus *Aneimites* from the lower Pottsville of West Virginia. They are usually borne singly at the apices of the slightly dilated terminal extensions of the outer pinnae, and show some slight indications of a pollen-chamber. They have been found only as impressions and therefore cannot be compared properly with the beautifully preserved foreign specimens showing internal structure. The author is of the opinion that the American form is more closely related to *Lagenostoma* than to any other cycadofilicinean type at present recognized as seed-bearing.—EDWARD W. BERRY.

<sup>32</sup> DERSHAU, MAX VON, Wanderung nukleolarer Substanz während der Karyokinese und in lokal sich verdickenden Zellen. Ber. Deutsch. Bot. Gesells. 22:400-411. pl. 21. 1904.

<sup>33</sup> RENNER., OTTO, Ueber Zwitterblüthen bei *Juniperus communis*. Flora 93:297-300. fig. 3. 1904.

<sup>34</sup> WHITE, D., Smithsonian Miscellaneous Collections 47:322-331. pls. 47-48. 1904.

PARTHENOGENESIS in *Wikstroemia indica*, one of the Thymelaeaceae, is announced in a preliminary paper by WINKLER.<sup>35</sup> The pollen develops imperfectly or not at all, and attempts to germinate the pollen by the usual methods were unsuccessful. Although pollination was prevented, embryos developed, and sections showed that the embryos arise from unfertilized eggs. The behavior of the chromatin will be studied later. Up to date the angiosperms in which parthenogenesis has been shown to exist are *Antennaria alpina*, *Alchemilla* (several species), *Thalictrum purpurascens*, *Taraxacum officinale*, *Hieracium*, and *Wikstroemia indica*. *Gnetum Ula* is the only gymnosperm in which parthenogenesis has yet been reported.—CHARLES J. CHAMBERLAIN.

OLSSON-SEFFER<sup>36</sup> has written a short defense of LINNAEUS, à propos of the recent Swedish biography by T. M. FRIES. The particular occasion for OLSSON-SEFFER's paper is a choleric and most unjust attack upon LINNAEUS by KALISCHER and HANSEN. Considerable attention is also paid to the unfair treatment which is accorded to LINNAEUS in SACHS's *History of Botany*. There can be no doubt that LINNAEUS has a secure place among the greatest botanists of all time, and the imputations that have been cast upon him are certain to be less harmful to the renown of LINNAEUS than to the reputation of his accusers.—H. C. COWLES.

INTERCELLULAR PROTOPLASM has been further investigated by KNY.<sup>37</sup> The principal material was cotyledons of *Lupinus albus* and *L. angustifolius*. That the protoplasm in the intercellular spaces is in direct communication with that of the neighboring cells is probable from the fact that the spaces contain starch grains. If there is protoplasmic continuity between the intercellular spaces and the neighboring cells the absence of nuclei in the spaces would not be strange. Perforations and connecting threads could not be identified positively. How the protoplasm gets into the spaces the author is not yet ready to explain.—C. J. CHAMBERLAIN.

THE PHYTON THEORY is supported by COL in a lengthy paper<sup>38</sup> which deals mainly with abnormally placed vascular bundles in dicotyledons. Starting with the Campanulaceae the author has extended his observations to a large number of families, and reaches the conclusion that the bundles in question are normal in part of their course, though frequently for only a short distance. The chief arguments advanced in favor of the phytion theory are (1) the bundles coming from the leaves diminish in volume as they descend through the stem; (2) practically

<sup>35</sup> WINKLER, HANS, Ueber Parthenogenesis bei *Wikstroemia indica* (L.) C. A. Mey. Ber. Deutsch. Bot. Gesells. 22:573-580. 1905.

<sup>36</sup> OLSSON-SEFFER, P., The place of Linnaeus in the history of botany. Jour. of Bot. 42:262-269. 1904.

<sup>37</sup> KNY, L., Studien über intercellulares protoplasma II. Ber. Deutsch. Bot. Gesells. 22:347-355. 1904.

<sup>38</sup> COL, A., Recherches sur la disposition des faisceaux dans la tige et les feuilles de quelques dicotylédones. Ann. Sci. Nat. Bot. 8: 20: 1-288. 1904.

all of the vascular formations of the stem supply appendicular organs.—M. A. CHRYSLER.

HOLLICK<sup>39</sup> has published further additions to the Cretaceous flora of Long Island, treating of plants from the Northport Clays and from the vicinity of Hempstead Harbor, Oyster Bay, and Montauk Point. Nine new species, including an interesting form of *Marsilia*, are described. The supposed palm *Serenopsis* is reconsidered in the light of better material and is definitely referred to *Nelumbo*. This leaves a species of palm (about to be published by the undersigned in *Torreyia*) coming from the mid-Cretaceous of Delaware and Maryland, as the earliest known plant of this type from American strata.—EDWARD W. BERRY.

NEWCOMBE,<sup>40</sup> in his presidential address before the Michigan Academy of Science, contrasts the old and new types of biological surveys, and makes a strong appeal for the new progressive and definite survey of the ecological type, accompanied by detailed maps, such as has been carried on by FLAHAULT in France, by the SMITHS in Britain, and begun in Michigan by LIVINGSTON. Concise statements are made concerning the uses of such a survey, both scientific and practical. It is much to be hoped that the plan here advocated will be carried out, not only in Michigan but in many other states as well.—H. C. COWLES.

LAWRENCE gives the results of his investigation of the apple scab in Washington.<sup>41</sup> He was able, as were CLINTON and others, to confirm the discovery made by ADERHOLD, that *Fusicladium dendriticum*, found as a parasite on the fruit and leaves of the apple during the summer, is but a stage in the development of *Venturia inaequalis*, the perfect form being found on the dead leaves as a saprophyte during the winter. He recommends that the fallen leaves should be gathered and destroyed and that the usual spraying with Bordeaux mixture be conducted in the spring.—E. MEAD WILCOX.

CHEMOTAXIS of the sperms of *Marchantia* toward a number of albumins, globulins, nucleo-albumins, proteids, and enzymes, is the subject of a paper by LIDFORSS.<sup>42</sup> Out of nineteen substances tested only two gave a negative result; all the others attract the sperms when in the right concentration. The author suggests that proteid substances are probably the main factor in the attraction of such sperms to the archegonia in nature, as well as in the tropism of pollen tubes. There is some evidence that *Marchantia* sperms are positively aerotropic.—B. E. LIVINGSTON.

<sup>39</sup> HOLLICK, A., Additions to the paleobotany of the cretaceous formation on Long Island. II. Bull. N. Y. Bot. Gard. 3:403-418. pls. 70-79. 1904.

<sup>40</sup> NEWCOMBE, F. C., A natural history survey for Michigan. Annual Report Mich. Acad. Sci. 6:28-36. 1904.

<sup>41</sup> LAWRENCE, W. H., The apple scab in western Washington. Bull. Wash. Exp. Stat. 64:1-24. figs. 1-5. pl. 1-2. 1904.

<sup>42</sup> LIDFORSS, B., Ueber die Reizbewegungen der *Marchantia*-Spermatozoiden. Jahr. Wiss. Bot. 41:65-87. 1904.



HUME<sup>43</sup> has published an account of observations and experiments regarding five serious diseases of the Irish potato that are known to occur in Florida: late blight, caused by *Phytophthora infestans*; early blight, caused by *Alternaria solani*; scab, caused by *Oospora scabies*; rhizoctonia blight, caused by a species of *Rhizoctonia*; and bacterial blight, caused by *Bacillus solanacearum*. A brief discussion of the nature and effects of each disease is accompanied by statements as to the proper methods of control to be employed in each case.—E. MEAD WILCOX.

FROM A consideration of the various causes assigned by different authors as inducing flower-formation, LOEW<sup>44</sup> believes that such causes have one common physiological factor, namely, an increased concentration of sugar. He advances the theory that flower-formation is a phenomenon of irritability; that a certain concentration of sugar in the plant stimulates the embryonic substance to differentiate male and female nuclei. Unfortunately, the evidence offered is very limited and not at all conclusive.—RAYMOND H. POND.

NATHANSOHN's last work on permeability of the plasmatic membranes of plants,<sup>45</sup> which was reviewed in these pages some time since,<sup>46</sup> includes in its discussion the results of a large series of experiments with the tissue of *Dahlia* tubers. The paper which embodied the details of this work, though actually published before the one already reviewed, has but recently come to hand.<sup>47</sup> Those interested in this subject will need to read the two papers together.—B. E. LIVINGSTON.

THE FIRST NUMBER of the second series of KARSTEN and SCHENCK's<sup>48</sup> *Vegetationsbilder* comes from the hand of ULE, the well-known student of the South American tropics. The number is devoted to the illustration of some characteristic epiphytes of the Amazon district, and the standard of the preceding numbers is fully maintained. Among the epiphytes figured are *Nidularium*, *Platyserium*, *Polypodium*, *Cereus*, and *Anthurium*.—H. C. COWLES.

THE INFLUENCE of weak aqueous solutions of ether upon the growth of *Spirogyra* has been studied by GERASSIMOW.<sup>49</sup> In these cultures many of the

<sup>43</sup> HUME, H. HAROLD, Potato Diseases. Bull. Florida Exp. Stat. 75:177-196. pl. 1-4 and frontispiece. 1904.

<sup>44</sup> LOEW, OSKAR, Zur Theorie der blütenbildenden Stoffe. Flora 94:124-128. 1905.

<sup>45</sup> NATHANSOHN, A., Weitere Mitteilungen über die Regulation der Stoffaufnahme. Jahrb. Wiss. Bot. 40:403-442. 1902.

<sup>46</sup> BOT. GAZETTE 38:477. 1904.

<sup>47</sup> NATHANSOHN, A., Ueber die Regulation der Aufnahme anorganischer Salze durch die Knollen von *Dahlia*. Jahrb. Wiss. Bot. 39:607-644. 1904.

<sup>48</sup> KARSTEN, G., und SCHENCK, H., Vegetationsbilder. Zweite Reihe, Heft 1. E. ULE, Die Epiphyten des Amazonasgebietes. Tafel 1-6. Jena: Gustav Fischer. 1904. Single parts M 4; to subscribers M 2.50.

<sup>49</sup> GERASSIMOW, J. J., Aetherkulturen von *Spirogyra*. Flora 94:79-88. 1905.

cells swell laterally and thus become barrel-shaped. Certain cells without nuclei increase in length but never swell in this way. Thus the author concludes that the swelling is brought about in some manner through the action of the ether upon the nuclear mechanism.—B. E. LIVINGSTON.

TSCHIRCH<sup>50</sup> finds that many dicotyledonous plants possess two types of root in the same individual, one sort having a nutritive function and the other serving to fasten the plant to the substratum. The so-called "fastening roots" are distinguished by the presence of mechanical fibers and generally by the absence of pith and by the larger size of the central cylinder.—M. A. CHRYSLER.

R. M. HARPER<sup>51</sup> has continued his valuable ecological and taxonomic observations on the flora of Georgia, a state whose botany has been peculiarly unknown until these and previously noted<sup>52</sup> studies were made. In addition to critical taxonomic notes, these papers contain accounts of the author's itinerary, together with landscape figures and ecological remarks.—H. C. COWLES.

EPIPHEGUS VIRGINIANA has been studied by COOKE and SCHIVELY,<sup>53</sup> who find that the parasitic haustoria arise from the roots of the host, the beech, and not from the parasite. As is usual in such plants, there is a precocious endosperm, and the embryo is rudimentary. Bicollateral bundles are found both in the tuber and in the aerial shoot.—M. A. CHRYSLER.

WOODRUFFE-PEACOCK<sup>54</sup> has published some rather peculiar suggestions on the study of rock-soil floras. An immense number of habitat types are proposed, but no attempt is made at analysis. It is obvious that the author is not conversant with modern ecological literature.—H. C. COWLES.

THE STRUCTURE and sprouting of the seed, and the structure of the mature plant of *Cassytha filiformis* are described by Miss BOEWIG.<sup>55</sup> This plant, though a parasite resembling *Cuscuta*, has functional chlorophyll tissue, especially when growing in the shade.—M. A. CHRYSLER.

TANSLEY<sup>56</sup> gives an account of the methods which he has employed in ecological surveying with his classes on the coast of Brittany. The scheme makes possible accurate and detailed mapping.—H. C. COWLES.

<sup>50</sup> TSCHIRCH, A., Ueber die Heterorhizie bei Dikotylen. *Flora* 94:68-78. 1905.

<sup>51</sup> HARPER, R. M., Botanical explorations in Georgia during the summer of 1901. *Bull. Torr. Bot. Club* 30:282-295, 319-342. 1903. Explorations in the coastal plain of Georgia during the season of 1902. *Bull. Torr. Bot. Club* 31:9-27. 1904.

<sup>52</sup> See *BOT. GAZ.* 34:386. 1902.

<sup>53</sup> COOKE, E., and SCHIVELY, A. F., Observations on the structure and development of *Epiphegus virginiana*. *Contrib. Bot. Lab. Univ. Penn.* 2:352-398. 1904.

<sup>54</sup> WOODRUFFE-PEACOCK, E. A., How to make notes for a rock-soil flora. *Rural Studies Series*, No. 5. Louth, 1904.

<sup>55</sup> BOEWIG, HARRIET, The histology and development of *Cassytha filiformis*. *Contrib. Bot. Lab. Univ. Penn.* 2:399-416. 1904.

<sup>56</sup> TANSLEY, A. G., A second experiment in ecological surveying. *New Phytologist* 3:200-204. 1904.

## NEWS.

DR. ERNST HALLIER, the mycologist, died at Dachau, near Munich, December 20, 1904, at the age of seventy-three.

DR. A. ERNST, formerly privatdocent at the University of Zürich, has been appointed professor and director of the botanical laboratories.

MISS CLARA E. CUMMINGS, of Wellesley College, went to Jamaica in February, to spend several months in a study of the flora, especially the lichens.

A. S. HITCHCOCK, of the Division of Agrostology, Department of Agriculture, has purchased the grass herbarium of F. LAMSON-SCRIBNER, containing many of his types.

DR. ERNST ABBE, of Jena, whose name is so well known in connection with the optical apparatus of the Karl Zeiss establishment, died January 16 at the age of sixty-four years.

SIR JOSEPH HOOKER retired from the editorship of the *Botanical Magazine* at the close of 1904, after forty years of service. He is succeeded by SIR W. THISELTON-DYER.

AT THE MEETING of the Linnean Society on December 15, 1904, fifteen ladies were elected Fellows. Among those thus honored were Miss MARGARET BENSON and Miss ETHEL SARGANT.

AT THE ANNUAL MEETING of the Torrey Botanical Club, held on January 10, H. H. RUSBY was elected president in the place of ADDISON BROWN, who resigned after fifteen years of service in that office.

JOHN F. CROWELL, director of the Buffalo Botanical Garden, will visit Panama during February and March as an agent of the New York Botanical Garden, which will undertake botanical explorations in co-operation with the engineers of the Panama Canal Commission.—*Science*.

PROFESSOR N. L. BRITTON, Mrs. E. G. BRITTON, Dr. C. F. MILLSPAUGH, and Mr. M. A. HOWE sailed in January to New Providence for a further botanical exploration of the Bahaman archipelago. Mrs. BRITTON will collect on New Providence, while the rest of the party will explore the Berry and Great Bahama groups.

THE MACMILLAN CO. announces for the spring a revised and enlarged edition with many new illustrations of CAMPBELL's *Mosses and ferns*. They will also publish a book by MAUD G. PETERSON entitled *How to know wild fruits*, which classifies wild plants by their fruits. They are also to publish a translation of COHNHEIM's *Chemistry of the proteids*, by Dr. GUSTAV MANN. The book will be of interest not only to chemists, but especially to biologists. The advance in the knowledge of proteids will be fully set forth.

## BOTANICAL GAZETTE

APRIL, 1905

CONTRIBUTIONS FROM THE CRYPTOGAMIC LABORATORY OF HARVARD UNIVERSITY. LX.

A NEW AMERICAN SPECIES OF WYNNEA.

ROLAND THAXTER.

(WITH PLATES IV AND V)

IN the third volume of HOOKER's *Journal of Botany and Kew Garden Miscellany* (1851) BERKELEY published a description without figures of a large and striking discomycetous fungus, distinguished by the possession of long ear- or spoon-shaped apothecia, arising in a fasciculate fashion from a well-developed common stem. This form, which was said to have been found abundantly on rotten wood near Darjeeling, India, he placed in the then very comprehensive genus *Peziza*, comparing it to *Peziza onotica* and *P. leporina*, and designating it as *P. macrotis*. Some years later, however, having received from Dr. CURTIS a closely related North American species collected by BOTTERI near Orizaba, Mexico, he was led to create the new genus *Wynnea* for the reception of these two forms (Jour. Linn. Soc. 9:1866), the Mexican species being used as the type under the name *Wynnea gigantea*. Both species were subsequently illustrated by COOKE in his *Micrographia*, the colors being no doubt guessed at from BERKELEY's descriptions and from the dried specimens. *W. macrotis* is here said by COOKE to occur also in Mexico, but no authority for this statement is mentioned. During the forty years that have elapsed since the collection of *W. gigantea* by BOTTERI, there seems to have been no further mention of the occurrence of these or of other species of *Wynnea*, and in more recent years the genus has been consigned to the limbo of synonymy by SACCARDO in his *Sylloge*, where both species are included in the genus *Midotis*.

In the summer of 1888, a portion of which was spent by the writer in collecting fungi among the mountains of Tennessee and North Carolina, a species of *Wynnea* was found near Burbank, Tennessee, growing on the ground in rich woods, in a single locality; where several clusters of its long bluntly pointed, rabbit-ear-shaped dark brown apothecia were scattered in a limited space, each cluster borne on a well-defined stout stem emerging directly from the humus. The resemblance of this plant to COOKE's figure of *Wynnea macrotis*, to which it closely corresponds in form and color, was so striking that it was assumed to be that species, despite certain differences in the size and appearance of the spores when fully mature, and in the absence of any authentic material of the Indian species for comparison it was so referred.

A second visit was made to the same region in 1896, and the *Wynnea* was again encountered, both at Burbank and at Cranberry, North Carolina; one of the specimens from the last-named locality being parasitized by a fine species of *Syncephalis* described in a former number of the GAZETTE (24:1. 1897) as *S. Wynneae*, the host being here recorded as *W. macrotis*. Having noticed, while gathering this material, that the stems appeared to have been broken from some attachment in every case, and not to have arisen like most humus *Pezizae* from an indefinite mycelium, a more careful examination was made in subsequent gatherings, and a little digging about the base of the stem showed that it originated in every case from a large, irregularly lobed, brown, firm, tuber-like body buried a few inches deep in the humus. This body, which was somewhat cartilaginous in consistency, showed, when cut, a chambered structure (figs. 5 and 6), the interior being traversed by light and dark more or less contrasting winding areas, closely resembling those characteristic of many *Tuberaceae* or *Hymenogastreae*; and at first sight it seemed not impossible that the *Wynnea* might actually be parasitic on some hypogaeous fungus. A microscopic examination of sections cut from this tuber, however, showed no signs of any structures which could by any possibility be considered to represent modified hymenia. The chambered interior, as is shown by the accompanying figures, is surrounded by an external layer or cortex of large, empty, thin-walled, brownish cells, those on the surface showing signs of degeneration

and wearing, which is rather abruptly succeeded by a peripheral region lying beneath it, composed of densely woven brownish filaments. As these filaments pass toward the interior, they become more loosely woven, the walls are much thickened, and the living protoplasmic contents are evident; the brownish tinge is lost as they pass into the white or colorless more or less gelatinous areas by which the adjacent chambers are separated. The chambers themselves show the greatest irregularity in contour, and are clearly marked off by a layer of dark cells which line them and contrast rather abruptly with the intermediate colorless areas above mentioned. These dark hymenium-like layers closely resemble the general external layer, and are made up of dark-walled, rounded, empty cells of somewhat smaller size, packed irregularly four or five deep; the somewhat ragged appearance of the superficial ones suggesting the lysigenous origin of the cavities which they line. Two such layers lying one on each side of an intermediate colorless region thus form the wall separating the cavities of two adjacent chambers (fig. 6). The early condition of this tuber-like body could not be determined, since all the specimens examined were well matured, and showed no signs of developing chambers. The body, however, appears to be in the nature of a sclerotium, which from its spongy structure may possibly serve the double purpose of supplying moisture as well as nutriment to the developing apothecia.

An examination of the specimens of *Wynnea gigantea* in the Curtis Herbarium shows that this species is characterized by a general habit closely resembling that of the Carolina form; and the main stem, where present in these specimens, is evidently broken from some attachment which may safely be assumed to have been a sclerotoid body similar to that above described. The presence of such a body might offer an additional reason for retaining BERKELEY's genus, but its characters seem otherwise quite sufficient to remove it from *Midotis* or other known discomycetous genera. In regard to *Midotis* it may further be said that no one appears to have any definite knowledge of this genus at the present time, and it is altogether doubtful what the nature of this generic type really is. The name is first mentioned by FRIES (Syst. Orb. Veg. 363), without further allusion to a specific form than the remark "Species unica pleuropus;" while

in the *Elenchus* (2:29), published five years later (1830), the first mention of the type species, *Midotis lingua*, appears. This fungus, which is described as growing "ad basos truncorum" and as possessing an *inferior* hymenium, has not been found again, so far as is known; and it seems quite uncertain what it may have been, or even if it were anything more than some well-known form growing under abnormal conditions. The only discomycete known to the writer which might be referred to *Midotis*, and which possesses a truly inferior hymenium, is a plant found growing on dead logs in September, 1889, near New Haven, and again at Burbank; the material in the former locality being rather abundant. The apothecia are very thin, broadly spathulate, proliferous, and fasciculate, having a habit of growth very like that of some basidiomycete; the spores small and insignificant, and the inferior hymenium very characteristic and by no chance accidental. This plant, which has been provisionally referred to *M. plicata* Cke. & Hark., may perhaps really be a *Midotis* in the Friesian sense, on account of the unusual position of its hymenium; but that the other species included in the genus by various writers really belong here seems doubtful. The only species among these for the most part tropical forms, that the writer has examined, is the Cuban *M. verruculosa* B. & C., in which it is not possible to determine whether the hymenium is inferior or not. The status of *Midotis* itself being thus decidedly uncertain, it seems doubly undesirable to include in it the members of what at least appears to be a well-marked and peculiar genus.

Within the past year Mr. MASSEE has been so kind as to send to the writer a small fragment of the type material of *Wynnea macrotis* and *W. gigantea*, and, as has already been mentioned, he has examined the specimens of the latter species in the Curtis Herbarium, which form a part of the original gathering of BOTTERI, and include one large and very well-developed example. None of these, however, correspond very closely to the figures given by BERKELEY and COOKE, the apothecia, though somewhat more blunt than in the Carolina form, hardly presenting the thin, broadly spathulate, and freely proliferous habit represented in these drawings. Mr. MASSEE informs me that in his opinion the Berkeleyan species are not specifically distinct, although the color and habit of the two are so very differently represented in the *Micrographia*.

A comparative examination of the spores in all three species shows that when fully mature all are characterized by the presence of longitudinal markings, apparently corresponding to slight depressions and somewhat roughened intervening elevated regions which extend the whole length of the spores. Although these markings are conspicuous in the Carolina species, they are hardly visible until the numerous oily globules with which the spores are originally filled (*fig. 4*, upper spore) have been obliterated by treatment with glycerine or otherwise (*fig. 4*, two lower spores). While they are much less striking in *W. gigantea*, they are nevertheless readily seen (*fig. 8*), but in the material of *W. macrotis* received from Mr. MASSEE, they are exceedingly faint, possibly owing to the fact that the spores may not have been thoroughly matured. In all three species the spores are characteristically inequilateral, being more strongly curved on one side than on the other, apparent deviations from this rule being probably in all cases due to differences in the point of view. While in *W. macrotis* and *W. gigantea* they are bluntly rounded, they are more or less conspicuously apiculate or papillate at each extremity in the Carolina species, and the spore as a whole is distinctly larger. The spores of *W. macrotis* sent by Mr. MASSEE (*fig. 7*) are slightly smaller than those of *W. gigantea*; but the difference is insignificant, and could not serve to distinguish the species in the absence of other distinctive characters. Nevertheless it seems more desirable to retain both the Berkeleyan species until further data may be obtained by a re-examination of fresh material.

For convenience of reference the original descriptions of BERKELEY are quoted below. The genus may be characterized as follows, the sclerotium of the Carolina form being assumed to occur in the other species as well.

WYNNEA Berkeley & Curtis, Jour. Linn. Soc. 9:124. 1866.

Apothecia thick, firm, subcartilaginous, tough and subcoriaceous on drying, erect, elongate, ear-shaped, simple or subproliferous, several- to many-clustered on a common stalk arising from a sclerotium buried in the substratum. Paraphyses cylindrical, simple or branched. Asci cylindrical, tapering to an elongated base penetrating the subhymenium with the filaments of which it is continuous, without articulation. Spores large, inequilateral.



WYNNEA GIGANTEA B. & C., Jour. Linn. Soc. 9:124. *pl.* 17. *fig.* 31. *Midotis gigantea* Sacc. Sylloge 8:547.

"Common stem three inches high, three-quarters of an inch thick, deeply rugose and cracked, so that the surface resembles that of *Opegraphae*; above divided repeatedly, with subdivisions elongated into ear-shaped cups, which are smooth externally, but wrinkled, though not cracked like the stem when dry; the cups are from two and one-half to three inches long, with incurved margins variously divided and sometimes proliferous. Asci cylindrical, containing eight subcymbiform spores .00095 inch long, and more or less obtuse at either end. When steeped in water, the inside of the stem acquires a slight foxy tinge. The substance is so totally different from *Peziza*, though this curious fungus is closely allied to *P. leporina* and *P. onotica*, that it cannot be placed in the same genus. *Peziza macrotis* Berk., a species found abundantly at Darjeeling at 7,500 feet, is clearly congeneric and may be characterized *Wynnea macrotis* Berk., etc."

Collected near Orizaba, Mexico, by BOTTERI, without note as to substratum.

#### WYNNEA MACROTIS Berk.

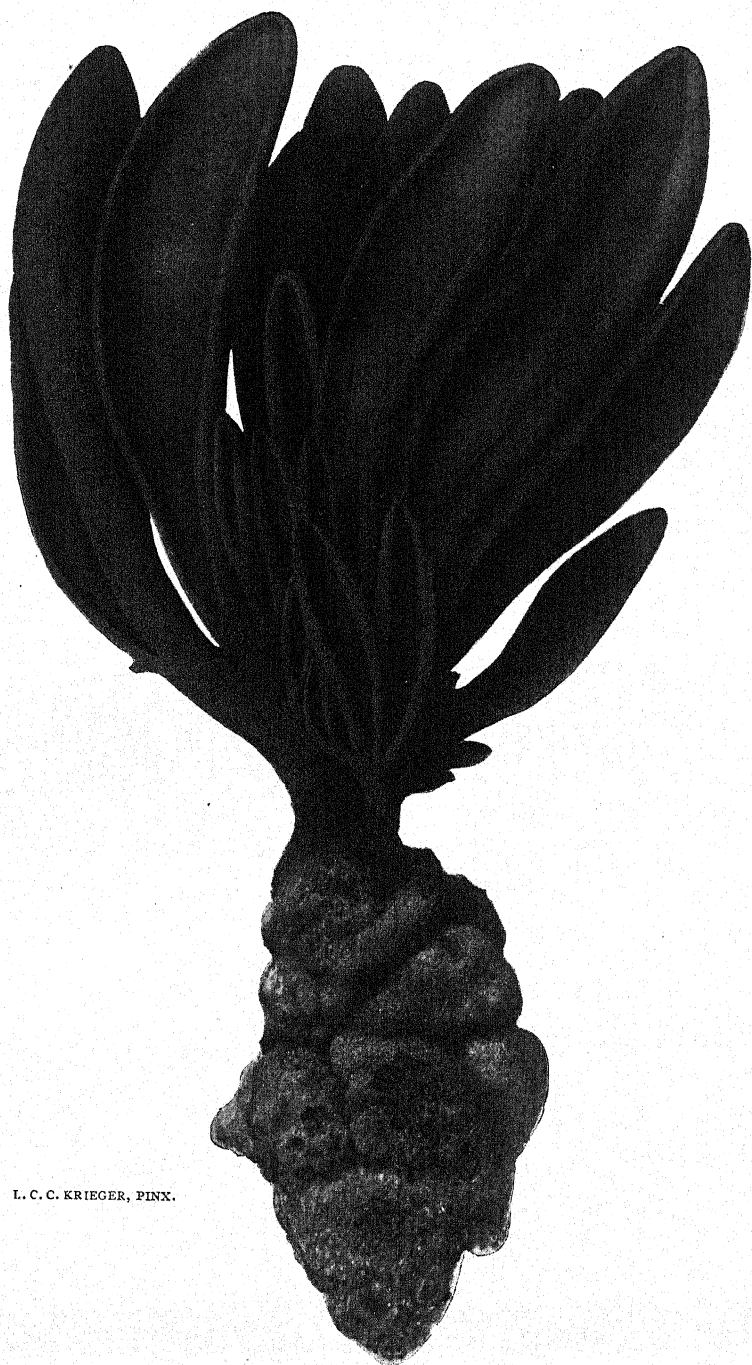
*Peziza macrotis* Berk., Hook. Jour. Bot. & Kew Gard. Misc. 3:203. 1851. *Wynnea macrotis* Berk., Jour. Linn. Soc. 9:124. 1866. *Midotis macrotis* Sacc., Sylloge 8:547.

"Inodorous, dry, firm, leathery, subcartilaginous, varying in size, sometimes five inches long; erect, tufted, connate below and thence branched; cups elongated, oblique auriform, of a bright liver color, smooth externally; margin subinvolute. Hymenium even, purplish. Sporidia oblong-elliptic, with one side in general more convex. Nucleus single, in dried specimens."

On rotten wood Darjeeling, India, 7500<sup>ft</sup>, June-July.

#### *Wynnea americana*, nov. sp.

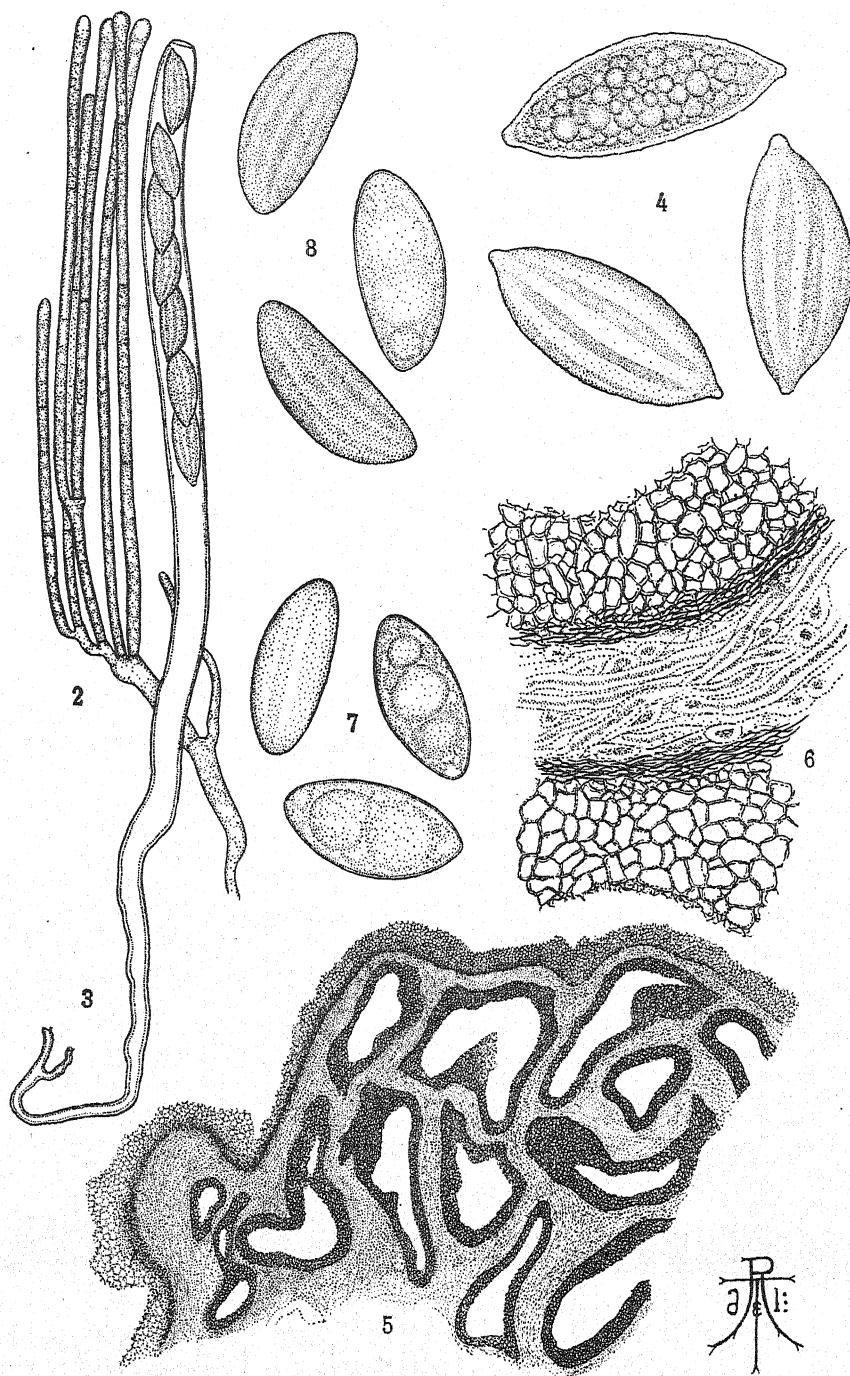
Sclerotium tough, subgelatinous, coriaceous on drying, irregularly lobed, variable in size, 50×40<sup>mm</sup> more or less, brown. Main axis becoming variously divided above almost immediately after emerging from the ground, the short divisions giving rise at once to clusters of apothecia of variable size and number. Apothecia several to about twenty-five on a single plant, typically simple, rarely proliferous, erect, elongate ear-shaped, very variable in size; the longest seen 130×60<sup>mm</sup>, the average about 80<sup>mm</sup>, the margins somewhat



L. C. C. KRIEGER, PINX.

THAXTER on WYNNEA





THAXTER on WYNNEA



involute on drying, the external surface rich blackish-brown, finely verruculose, the roughness due to projecting groups of irregular parenchyma-like cells becoming somewhat hair or chain-like toward the margins. Hymenium even, dark dull purplish-red, or brown. Asci elongate, about  $500-540\ \mu$  long, the sporiferous part cylindrical, about  $18\ \mu$  in diameter. Paraphyses septate, simple or irregularly branched, clavate, the slightly brownish terminal enlargement more abruptly and conspicuously distinguished in older specimens. Spores eight, subcymbiform,  $32-40 \times 15-16\ \mu$ , the extremities apiculate or papillate; marked when mature by about eight roughened areas running longitudinally and separated by a corresponding number of smooth slightly depressed areas, the spore when fresh completely filled by numerous small round refractive oily masses.

Growing on the ground in rich woods, Burbank, East Tennessee, and Cranberry, North Carolina.

Professor DURAND has kindly allowed me to examine a specimen collected by E. WILKINSON at Mansfield, Ohio, and communicated by Professor KELLERMAN, which corresponds in all respects with the Carolina plant. The spores of BERKELEY'S species differ in shape and in their smaller size; those of *W. gigantea* measuring  $25-30 \times 12\ \mu$ , and those of *W. macrotis* received from Mr. MASSEE  $20-25 \times 11-12\ \mu$ . The apothecia of *W. gigantea* seem also to be somewhat smaller, more rounded distally, more numerous in a single plant, and distinguished by their much paler color.

HARVARD UNIVERSITY.

#### EXPLANATION OF PLATES IV AND V.

FIGS. 1-6.—*Wynnea americana* Thaxter.

FIG. 1. General habit of a well-developed plant. For the original of this figure, done in color by Mr. KRIEGER from a formalin specimen and colored sketches of my own from fresh material, I am indebted to Professor FARLOW.

FIG. 2. Paraphyses.

FIG. 3. An ascus showing connection with subhymenial filament.

FIG. 4. Three spores, the upper in optical section.

FIG. 5. Portion of a section of the subterranean sclerotium showing chambers and cortex. Leitz obj. C+oc. 1.

FIG. 6. Portion of walls between two chambers. Leitz obj. 1+oc. 1.

FIG. 7. *W. macrotis* Berk. Three spores, two in optical section.

FIG. 8. *W. gigantea* Berk. & Curt. Three spores, one in optical section. The spores were drawn with Zeiss apochr. 1.25<sup>mm</sup> and 4 ocular.

# ON THE DEVELOPMENT OF HAMAMELIS VIRGINIANA.

CONTRIBUTIONS FROM THE BOTANICAL LABORATORY OF  
JOHNS HOPKINS UNIVERSITY, No. 3.

D. N. SHOEMAKER.

(WITH PLATES VI AND VII)

## INTRODUCTION.

THIS work on *Hamamelis* was undertaken on account of its peculiar habit of flowering. It is one of the few angiosperms that flowers in the fall and matures fruit the following year. This peculiarity made it seem worth while to investigate its entire embryological history, and especially the behavior of the pollen tube and the time and manner of fertilization. The subject was suggested by Dr. D. S. JOHNSON, to whom I wish to express my gratitude for sympathetic guidance and instruction during its prosecution.

The literature of the family is not extensive, and none of it has to do with the embryology of any of its forms. The most complete working out of the anatomy and affinities is by REINSCH (12). BAILLON (3) carefully described the organogeny of the flower in *Hamamelis virginiana* and *Fothergilla Gardeni*. VAN TIEGHEM (14) worked on the secretory canals of *Liquidambar* and *Altingia*. THOUVENIN (13) described the structure of the root, stem, and leaves of various members of the family. The account given by NIEDENZU in Engler and Prantl's *Natürlichen Pflanzenfamilien* is the most complete I have seen.

In some American oaks, which require two years to mature seed, it has been found that fertilization takes place about a year after pollination. The statement is made by GOEBEL (15, p. 392) that a period of rest occurs after the pollen tube has reached the embryo sac in *Ulmus*, *Quercus*, *Fagus*, *Juglans*, *Citrus*, *Aesculus*, *Acer*, *Cornus*, and *Robinia*. As Miss BENSON (4) points out, this statement is erroneous in the case of British Amentiferae. It is not true of *Hamamelis*.

In *Colchicum autumnale*, according to HOFMEISTER (7), the pollen



tube reaches the embryo sac at the latest by the beginning of November, and it is not until May of the next year that the embryo begins to form. This plant and the autumn-flowering species of *Crocus*, like *Hamamelis virginiana*, bloom and shed their pollen in the fall. HOFMEISTER'S account of *Colchicum* shows that it differs essentially from *Hamamelis* in the behavior of the pollen tube and the time of fertilization. The other genera named as having a longer or shorter period between pollination and the beginning of embryonic growth are all pollinated in the spring, so that the resting period for most of them does not extend through the winter.

The family of the Hamamelidaceae comprises some fifty species, in eighteen genera, of which eight are monotypic. North America has three representative genera: *Hamamelis*, *Liquidambar*, and *Fothergilla*. The first is found nearly always in such sheltered places as harbor *Polystichum acrostichoides*, from Labrador to Florida and west to the Mississippi River. The second is found on the coastal plain and on bottom lands from New York to Florida, thence to Central America, and up the Mississippi River to southern Indiana. The third is found from Virginia to Florida, east of the Appalachian Mountains. *Hamamelis* has two more species, one in southern China and one in Japan; *Liquidambar* is also represented by two species which occur in southern Asia from Asia Minor to Formosa; and *Fothergilla* is represented by one other species in Persia. The remaining genera are confined to southern and eastern Asia and Malaysia, with the exception of three genera found in Madagascar and southern Africa. Thus the whole family, with the exception of three genera, is confined to the eastern and southern parts of North America and Asia. This peculiar and as yet unexplained distribution occurs in a large number of genera, but this family is one of the most pronounced cases found. It should also be said that *Hamamelites* and *Parrotia* are found in the Dakota group of the Cretaceous (9), and that *Hamamelis* (5) and *Hamamelidanthium* are found in Eocene strata in northern Europe, so that the family had formerly a much more extended range than at present.

I have usually found *Hamamelis* on rather steep hillsides with a northern exposure, or more rarely on low ground along streams. It is said to grow abundantly on mountain tops in Pennsylvania



and western Maryland, and COWLES (6) reports it as growing on sand dunes near Chicago. From his description, however, it is doubtful if the seed had germinated in these dry localities. It has thus a very restricted range, and seems to grow only in positions in which moisture is abundant and transpiration slow. *Liquidambar* is confined to alluvial soils and moist situations, and so follows river valleys and coast lines; its northern limit is the valley of the Hudson River in New York. *Fothergilla* grows in moist places.

The material of *Hamamelis virginiana* and *Liquidambar* for the present work was obtained from the region about Baltimore, from northern Virginia, from Long Island, and from southwestern Ohio. I am indebted for exotic forms to the kindness of Mr. GEO. V. NASH, of the New York Botanical Gardens, and to Mr. J. G. JACK of the Arnold Arboretum, Jamaica Plain, Mass. The long period of development made it necessary to collect nearly every week of the year for *Hamamelis*. Material of *Fothergilla* was collected in central South Carolina.

Killing and fixing was mostly done with a sublimate-acetic mixture made by adding 5 per cent. glacial acetic acid to a saturated aqueous solution of corrosive sublimate; this was often used hot. The material was cleared in xylol and imbedded in paraffin; and sections were cut 5 to 15  $\mu$  in thickness. For staining, a combination of haem-alum and Bismarck brown was tried, but Flemming's triple stain was found more satisfactory and was used almost exclusively. It was necessary before the young carpels could be sectioned in paraffin to remove carefully and laboriously the hairs from their bases, as on account of their thick walls the hairs could not be cut in paraffin, invariably tearing the sections. To avoid this process celloidin imbedding was used in a few instances, but it was impossible to get the sections thin enough for most purposes.

#### ORGANOGENY OF THE FLOWER.

The flower buds arise from axils of the leaves of the current year, or from latent buds of the two preceding years, and appear early in May. They, as well as the leaf buds and the young twigs, are covered by a dense coating of tufted hairs. Each hair develops from a single epidermal cell, which protrudes from the surface and is cut by anti-

clinal walls into four to twenty cells, each of which sends out a long process, making a many-rayed star. They are often raised on a low multicellular papilla.

Each flower bud produces a head of two to four flowers, and there are often as many as three buds from an axil. At first the tip of each bud is protected by three or four alternate bracts, which are soon left below on the stem of the flower head and finally fall off. The first floral organ to appear is the outside bract of each flower. As the buds grow the other two bracts arise successively, one on each side of the flower. The sepals appear in pairs, the first pair being anterior and posterior. The petals then arise in one cycle of four rudiments, inside which two successive alternating cycles of four rudiments each develop. The outer cycle, opposite to the lobes of the calyx, becomes stamens, the inner sterile staminodes.

The torus by this time, through unequal growth, has become concave, and on its floor are developed two horseshoe-shaped ridges, one anterior and one posterior. These grow together on the median line, and this line of fusion is carried upward by growth, so that there is a solid wall between the cavities of the carpels for a short distance. The carpels have separate styles and stigmas, but are united throughout their hollow portions. In each ovary there is found one ovule, which is suspended from the margin of the carpel. This development of the flower is essentially as described by BAILLON (3), except that he describes the ovary as originally having two ovules, one of which nearly always atrophies. LE MAOUT and DECAISNE (16) also figure a cross-section of the fruit showing two mature seeds in each carpel. Although I have examined several hundred carpels I have found but a single one with two ovules. BAILLON (17) also speaks of *Hamamelis* as being polygamous, but of this I have seen no evidence in my material. It is possible that these conditions may occur more frequently in places from which I have no material, or in other surroundings, yet the form has been very constant from all my collecting points.

In the mature flower the temporary parts, the stamens, petals, and nectaries, are smooth. The outside of the sepals and bracts, and the bases of the carpels are thickly covered with hairs. *Figs. 8 and 9* show how the rudiments of the growing flower fit together, and

how the bud is protected by its hairy covering. Most of these hairs have a double function. While young they act as slime cells in keeping the growing point and growing tissues moist, this function being best performed by the hairs on the tips of the sepals and bracts, and the bases of the carpels. These young hairs are long and tortuous, and wind among the growing rudiments (*fig. 9*). Their cavities are full of sap, and their nuclei take a very dark stain; they remain in this active stage longer than hairs on other parts of the plant. As they grow older all the hairs acquire thick cell walls, and tend to straighten. In their mature state they act as a protection against moisture. This function they perform by means of a waxy covering which repels water, so that it is very difficult to moisten a young flower bud, or a growing twig, or fruit; but if these hair-covered parts be soaked a short time in strong alcohol, and allowed to become dry again, they may be very readily moistened.

#### POLLEN SACS AND POLLEN.

Each fertile stamen rudiment begins early to form two microsporangia. There is apparently no evidence of the presence, at any stage, of the other two microsporangia that are usually found in angiosperms. No indication of pollen-formation is ever seen in the sterile rudiments.

The first evidence of the formation of the archesporium is found about the middle of June. The subepidermal layer divides by periclinal walls at the place where the microsporangia are to be formed (*fig. 1*). The exact derivation of layers is hard to trace, but it is quite certain that it is from the inner layer thus formed that all the archesporial tissue comes. By the middle of July the archesporium is well blocked out, and shortly after the spore mother-cells are formed. At this stage there is about them a moderately well-defined tapetum, and the outside wall of the microsporangium is three or four cell layers in thickness (*fig. 2*). Here the pollen mother-cells are only noticeable by their slightly larger nuclei and more deeply staining contents.

The further growth of the microsporangium is brought about by the increase in size of its cells, both sporogenous and tapetal. Before the tetrad division, the nuclei of the tapetum divide without

the formation of cell walls, and the tapetal cells have two or three nuclei each; the nucleoli also increase notably, and the contents of the cell become more largely vacuolate (*fig. 3*). The pollen mother-cells thicken their walls, and soon float freely in the cavity of the anther; increasing further in size, with a much larger nucleus and nucleolus (*fig. 29*). The two tetrad divisions occur almost simultaneously, although stages are found showing two nuclei (*fig. 30*). In the tetrad division the nuclear processes do not show at all clearly, though there seem to be fibers connecting the nuclei in one stage observed (*fig. 31*). The pollen grains have cell walls and but one nucleus when the mother-cell wall is broken down (*fig. 32*) and the grains released into the cavity of the microsporangium. The mature grain was described by VON MOHL, very briefly, in 1835. It has the shape of an oblate spheroid, with three meridional furrows (*fig. 33*); between these furrows the surface is covered by a fine reticulation. An equatorial section shows that the intine is strongly developed under the furrows, which gives the section of the interior a decidedly three-lobed appearance (*figs. 33 and 34*).

Soon after the pollen grain is freed from the mother-cell, its nucleus divides, and the smaller nucleus, probably the generative, retires into the extremity of one of the lobes. Here it becomes closely applied to the intine and is cut off from the larger cell by a very noticeable wall, which is probably of cellulose (*fig. 33*). Shortly before the pollen is shed this wall disappears, and the two nuclei then lie free in the cavity of the grain. The larger of the two, the tube nucleus, is loosely vesicular, while the structure of the generative nucleus is dense and deeply staining (*fig. 34*).

Of the four layers in the microsporangium wall only the subepidermal layer has any part in the opening of the anther, becoming the fibrous layer and covering the inner and lateral faces of the anther (*figs. 5 and 6*). The first and for a long time the only evidence of the differentiation of this layer is the radial lengthening of the cells. At this stage it is possibly not inappropriate to mention an instance of regeneration observed in this fibrous layer. From some unknown cause, the first subepidermal layer had been destroyed over a small area. The remaining part of that layer had developed normally. Into this gap tissue had grown from both sides, but that which came

from below was slight in amount, and had retained its original character; while the epidermal cells had greatly elongated and had divided into epidermal and secondary fibrous layer cells (*fig. 4*). These secondary fibrous layer cells resembled very closely at this stage those of the primary fibrous layer, and I see no reason to suppose that they would not have developed fibers at the proper time. Here then the epidermis seems to have been more plastic under the injured spot than the deeper lying tissues.

The fibers are developed in this layer shortly before the time the anther is to open, appearing on the side and bottom of each cell. Around the top, posterior, and bottom of the microsporangium there is a groove (*figs. 5 and 7*), and in the bottom of it the cells have no fibers and are quite thin-walled, so that they readily break, thus forming the line of dehiscence of the anther. As LECLERC DU SABLON (8) has shown for anthers in general, the opening is due to unequal shrinkage of the two walls of the fibrous layer. The outer wall being of cellulose, shrinks more on drying than the inner wall, which is strengthened by its lignified fibers. By this means the whole outer covering is bent upon itself and points directly toward the carpels (*fig. 7*); nearly all of the pollen adheres to these wings, and so is placed in the way of any insect that comes to visit the nectaries. The stigmas are ripe for pollination at the same time that the anthers open. Any insect visiting many flowers in succession must scatter pollen promiscuously, so that there is sufficient adaptation to insure cross-pollination, but no well-developed mechanism to prevent self-pollination. Pollen is ripe and begins to be shed in the latter part of October, and is shed from that time on into the winter, as the flowers keep opening with each return of warm weather, even as late as January.

#### OVULES AND EMBRYO SAC.

The ovules show specialization of archesporial tissue at the tip of the nucellus before the integuments have begun to develop, but it is very difficult to distinguish archesporial cells, although there seem to be several of these, each one cutting off a tapetal cell which divides repeatedly. The cells of this tissue then elongate in the direction of the long axis of the nucellus, and bury the mother-cells by some eight layers of cells in the nucellus.

It is also probable that this part of the nucellus forms the extremity of the conducting tissue for the pollen tube. In early stages three to five macrospores can be seen, but only one germinates. This goes through the usual stages, the resulting nuclei being arranged in the order most often found among angiosperms (*fig. 10*). The antipodals very early disappear, so that they are hard to find at the time of fertilization. The endosperm nucleus is found about the middle of the sac.

The tissue surrounding the mature embryo sac is much disintegrated (*fig. 10*). Around the chalazal end of the sac the tissue always stains deeply, and there is a quite evident strand of conductive tissue from the tip of the fibrovascular bundle at the chalaza to the lower end of the embryo sac (*fig. 10*). The base of the nucellus shows by its smaller cells that it is the most rapidly growing part. The development which the ovule has attained at the beginning of winter is shown in *fig. 11*. The integuments up to the early part of April are still behind the nucellus in growth; in spring their growth is hastened and they soon project beyond the nucellus, leaving a wide open micropyle (*fig. 21*). This is finally closed to a slit-like fissure between the edges of the outer integument.

The outer integument is now quite thick, formed of about eight layers of cells, and is uniform in structure throughout. The inner integument is made up of three layers of cells which are very much alike. The epidermal layer of the nucellus has already become slightly different from the underlying tissue.

#### POLLEN TUBES ARTIFICIALLY GROWN.

Pollen taken from open anthers was very readily sprouted in a 16 per cent. sugar solution made with tap water, in which 1.5 per cent. gelatin was dissolved. The pollen grains first became spherical by the filling out of the furrows, thus using the masses of intine on the inner sides of the furrows. Tubes sprout from the pollen grains when placed in the nutrient gelatin in one to three hours, and always arise from the smooth bands. The cultures were kept at room temperature and growth was more luxuriant in the dark. The growth of molds, etc., usually disturbed the cultures at the end of a few days.

The behavior of the nuclei was not readily observed. Methyl-green-acetic-acid was used to kill the pollen tubes, and no more

than two nuclei were ever found in a tube. The tubes showed a marked tendency toward the formation of cellulose plugs (*fig. 12*). It rarely occurred that part of the contents of the tube was in this way shut off, as the spaces walled off by plugs were mostly empty.

In the course of about three days' growth the pollen tube frequently "encysted" (*fig. 35*), that is a spherical swelling developed at the tip or near the tip of the tube into which nearly all the contents of the tube were withdrawn, including one or both nuclei. A wall was then formed completely closing off the swelling, which was often as large as the original grain. I have not determined the exact conditions which called forth this action, neither have I found such things in the style in normally grown pollen tubes. Miss BENSON (4) reports a case of somewhat similar character as occurring in *Carpinus*, though the spherical character and the separating wall were not nearly so pronounced. She suggests that this may be of use in the short resting period of this form, but was not able to find such appearances in the style.

The pollen showed ability to sprout at room temperature whenever the flowers opened. A collection made in Ohio early in January, after the unopened buds had endured a week of very cold weather, when the temperature had been as cold as  $-15^{\circ}$  F., sprouted in a seemingly normal way, though not so vigorously as earlier. I am inclined to think, however, that pollen shed so late never functions.

#### CONDUCTIVE TISSUE OF THE STYLE AND OVARY.

By the folding of the carpels each style has a groove formed, which leads from the stigma to the ovary. It is open at the top, and where its sides are slightly separated and its inner surface thus exposed, it bears the loosely arranged papillose cells of the stigma. The epidermis of the groove and two subepidermal layers continue this stigmatic tissue down to the base of the funiculus, the strand of conducting cells getting gradually deeper and deeper in the tissue of the style. The cell walls of the strand are thickened, partly gelatinized, and the contents of the cells are dense. *Fig. 13* shows its appearance and position about midway in the height of the style, and its course in longitudinal section is shown in *fig. 18*. When the flower first opens, the epidermis of the funiculus is not yet differentiated,

but as winter approaches the base of the funiculus becomes glandular. The epidermal cells enlarge, the walls thicken, and the contents become vacuolated. In the spring this process is carried still farther, and as the ovule occupies more and more of the cavity of the ovary, these cells secrete a mucus which fills the small remaining cavity around the base of the funiculus (*fig. 10*).

#### THE DESCENT OF THE POLLEN TUBE.

The pollen grains begin growth very shortly after falling on the stigma, and the growth is at first comparatively rapid. Its course is readily traced in the conducting tissue of the style, which is greatly disorganized by the growth of the large number of tubes usually present. The course is between the cells rather than through them. By the time that winter sets in the living part of one or more tubes is to be found in the neighborhood of the base of the funiculus (*fig. 11*). There are usually several living tubes at varying heights in the style at this time (*figs. 17 and 18*), and evidence of many more which have been stranded above. The unprotected tip of the style is dead and withered, while that part which is clothed with hairs is alive. It is in this protected part of the carpels that the pollen tubes hibernate. Soon after pollination the flower head twists on its stalk so as to invert the blossoms. The inverted calyx then very effectually protects the carpels from rain, sleet, and snow.

The pollen tubes found at this time are usually of greater diameter than at the beginning of growth. Tubes grown in sugar-gelatin solutions are 5 to 8  $\mu$  in diameter, and those which sprout on the stigma are at first about the same size; but those found during the resting stage are 12 to 15  $\mu$  in cross-section, and the wall is thicker than at first (*fig. 14*). The nuclei found did not exceed two in any tube.

When growth is renewed in the spring, the area of conducting tissue in the funiculus being increased, the pollen tube is soon seen in the cavity of the ovary. More than one tube may reach the ovary. At first the ovule is by no means ready for fertilization, and the integuments have not yet closed up the micropyle (*fig. 21*). The tubes do not appear at this time to have any definite direction of growth, but grow down beside the ovule or into the wide open



micropyle, or between the integuments. The course to the egg cell is through the micropyle and into the tip of the nucellus through the tissue derived from the tapetal cells, which stains deeply at the time and is probably conductive tissue. Thus it is seen that the tube grows just about as fast as the conductive tissue is prepared for it, and stops in the fall when it reaches the end of the mature conductive strand. The transference of the male nucleus has not been observed, but fertilization takes place about the middle of May, which is from five to seven months after pollination.

#### ENDOSPERM.

The antipodals very early disappear. The first result of fertilization is apparent in the action of the endosperm nucleus, which immediately begins to divide. The stage of free endosperm nuclei is very short, as cell walls have appeared in the twelve-nucleate stage. These walls first arise in the bottom of the embryo sac. Both endosperm and nucellus grow rapidly from this time forward. The endosperm early disintegrates the neighboring nucellar tissue except at two points, the tapetal strand of tissue leading down from the micropyle and bearing the fertilized egg at its lower end, and the pit at the chalazal end of the embryo sac which earlier held the antipodals. This and the deeply staining tissue surrounding it resist the action of the endosperm for some time, and by the growth of the base of the nucellus are pushed into a position on the side of the growing endosperm (*fig. 23*). This antipodal pit is finally absorbed.

The nucellus keeps pace with the growing endosperm, its epidermal layer being changed to make part of the inner seed coat. The differentiation of this layer is shown mainly by the larger size of its cells, especially at the tip of the nucellus, and by the crowded cell contents which take up blue stains very readily. This layer is the only part of the nucellus that permanently resists the action of the endosperm, and it is completed across the region of the chalaza so that it entirely surrounds the endosperm. Its nuclei are usually applied to the outer cell wall, and help doubtless in making the clear membrane which surrounds the nucellus in the mature seed. It is thrown into folds shortly before the ripening of the seed (*fig. 20*). The endosperm

is finally stored with food in the form of proteid grains, which shortly before ripening show numerous globoids (*fig. 22*) that disappear later. The ripe endosperm contains in its cells much oil along with proteid material, and in the cell walls there are imbedded numerous crystals of calcium oxalate (*fig. 15*). \*

#### THE EMBRYO.

The embryo begins growth comparatively late, so that the endosperm has already acquired some size before the first division of the egg occurs. The egg after fertilization becomes slightly imbedded in the tissue of the tapetal strand, and enlarges greatly. The first division is transverse and cuts off a small cell below and a large one above. By this continued cross division the suspensor may have five or six cells (*fig. 23*). The first division of the embryo is longitudinal. The embryo dissolves the endosperm in much the same way as the endosperm dissolves the nucellus, and lies free in a cavity formed by the disintegration of the endosperm. At maturity there is a straight axial embryo which extends from end to end of the seed and is richly stored with oil and proteid material in all its cells. The upper side of the cotyledons has already a well-developed palisade layer (*fig. 24*).

#### INTEGUMENTS.

The inner integument is at the beginning three cell layers in thickness, the innermost layer taking part in the formation of the inner seed coat. It early becomes filled with dense contents that stain blue readily (*fig. 20*), and finally shrink and become applied to the inner cell wall. The remaining layers are crumpled up so that they can only be made out with difficulty.

The outer integument thickens greatly, and its cells elongate, taking a curved oblong shape. The cell walls then begin to thicken and the whole integument forms the outer seed coat which is moderately hard, black, and very resistant to water. The outer integument is very smooth over the whole surface, except at the place of attachment of the funiculus, where there is a white saddle-shaped scar. The seed is ovoid, but very decidedly pointed at the lower end. The shape of the seed is a very important part of the discharging mechanism.

## THE CARPELS.

At blooming time the carpels are very slightly imbedded in the tissue of the torus (*fig. 17*). There is a very short calyx tube, however, shown in the figure below the attachment of the anther. As the fruit matures, the calyx tube lengthens proportionately more than the carpels, and this gives the fruit the appearance of being half buried in the torus (*fig. 38*). A longitudinal section (*fig. 39*) shows that this is only apparent and that the fruit is only slightly buried.

The substance of the carpels develops into two tissues, the outer one becoming fleshy with numerous roundish stone cells, the inner one forming part of the mechanism for expelling the seed. In each carpel this inner layer is formed in two halves, which are not closed at the top and are higher toward the posterior of each carpel, as shown in side view in *fig. 42*. These halves are never closely joined on the inner sides of the carpels, and there is provision for a split along the dorsal line also. The cells are developed into fibers diagonally from the inner edge to the dorsal line of each carpel, parallel to the top of the layer. In opening, this layer splits down the midrib of the carpel and in front. It then opens at the top and each half below begins to contract in a transverse direction. The cross-section of the opening layer is shown before contraction in *fig. 40*, after the opening of the fruit in *fig. 41*. The pressure exerted comes gradually on the seed, and it is thrown out, not by a sudden movement of the capsule, as in many such contrivances, but by being pinched on the smooth pointed lower end. The great smoothness of the seed and of the inside of the capsule assists greatly in the process. The seeds are often thrown to a distance of twenty feet. This movement is caused by drying, as can be proved by placing an opened capsule in water, when after some hours it will close entirely, and will open again on being dried.

## GERMINATION.

The seed thus distributed lies on the ground for two winters according to BAILEY (1), sprouting the second year. Under trees which fruited abundantly in the fall of 1901, but where the crop was a failure in 1900, it was not possible to find young seedlings in May 1902, though many seeds were found. Under trees which fruited

in 1900 it was easy to get young seedlings in various stages. The cotyledons remain in the seed coats until they have absorbed the stored up nourishment of the endosperm (*fig. 16*); they are then freed and exposed as green assimilative leaves. Attempts at sprouting the seed in damp sphagnum were made in the laboratory. The seed was planted in September of 1900, and by May of 1902 had just begun to protrude the tips of the radicles. They had been in the temperature of an unheated room constantly, but had not been subject to frost, and had never been allowed to dry out.

#### HAMAMELIS ARBOREA.

I procured one stage of the Japanese species *H. arborea* in the latter end of October. This differs from *H. virginiana* in its time of flowering, which is in very early spring. A variety, *H. arborea zuccariniana*, flowers as early as February, and thus approaches the flowering time of the American species. The flowers are in about the same condition in October as those of *H. virginiana*, except that the stamens are rather backward. The pollen grains are free and have each two free nuclei, and evidently pass the winter in that stage (*fig. 36*). As the pollen is shed in March at the latest, it probably must rest about two months before fertilization occurs. The petals are coiled involutely in the bud as in *H. virginiana*, but instead of being entirely smooth have a tuft of hairs on the tips. In other respects the two genera are much alike in their development so far as studied.

#### FOTHERGILLA GARDENI.

An incomplete series of stages of this species was studied. Its flowers appear in the spring along with the leaves. It lacks a corolla, and its calyx tube is much longer than that of *Hamamelis*, having five to seven very small teeth. The development of the stamens is described by BAILLON (3). They arise first as five single rudiments, which are followed by other rudiments on each side, so that there are finally five groups of five or six stamens, those of each group being of different ages and different heights. They pass the winter in the pollen mother-cell stage. At the time of flowering the ovules are not yet ready for fertilization, so that the pollen must have a resting period of nearly a week. The anthers have four microsporangia and

open by two valves instead of one, very much as is common in most angiosperm stamens which open by slits. The structure of the seed and fruit is like that of *Hamamelis*, except that the seed is smaller.

CORYLOPSIS PAUCIFLORA.

Only one stage of this species was examined. It was obtained in the spring before the flowers open, which occurs before the leaves appear. They are borne in drooping racemes, with many bracts, which are smooth outside, but covered by silky hairs within. The structure of these hairs is much like that in *Hamamelis*, but they are not rigid. The stamens, which have four microsporangia, pass the winter containing nearly mature pollen grains (*fig. 37*), with two free nuclei. The ovule passes the winter in the same stage as does that of *Hamamelis* (*fig. 25*). It is difficult to determine whether there is present a definitive macrospore or a macrospore mother-cell; however, there is no evidence of the presence of more than one macrospore mother-cell. There must also be some time here between pollination and fertilization.

LIQUIDAMBAR STYRACIFLUA.

Liquidambar is not so closely related to *Hamamelis* as the other genera studied. The buds in this species pass the winter with the merest rudiments of the floral organs present. The stamens are only small protuberances which do not show any archesporium. The mature anthers have four microsporangia and open by slits (*fig. 26*). The fibrous layer is very slightly developed as compared with *Hamamelis*. The flowers are imperfect, with rudiments of stamens appearing as nectaries among the flowers in the female heads. These were formerly thought to be both petals and stamens; abortive pollen is sometimes developed in them, which is evidence of their staminal nature (*fig. 27*). The carpels, which occur in pairs as in *Hamamelis*, are collected into large heads containing thirty-five to fifty flowers each. Each carpel has a double row of ovules developed on marginal placentae, and a broadly expanded stigmatic surface. With very rare exceptions, only one of these many ovules is fertilized, and this one is near or at the bottom of the cavity. There is a week or ten days between pollination and fertilization in this case. The developing seed shows the same resistant tissue at the antipodal

end of the embryo sac as is found in *Hamamelis*, but here it persists into the ripe seed. The epidermal layer of the integument is not used up, and around the chalaza there is a small fragment of the nucellus left in the ripe seed. This is never stored with food materials, and so cannot be called perisperm (*fig. 28*). The macrospore is buried about as deeply as in *Hamamelis*. It germinates only in the lower ovules, the upper ones never showing typical embryo sacs and being less developed progressively toward the top of the ovary. In the sterile ovules the cells of the outer integument become very much enlarged and at last empty. The substance of the nucellus is absorbed, and the ovules become polygonal bodies, resembling sawdust, which fill the upper part of the ovary. The outer integument of the fertile ovule (*fig. 28*) grows into a wing. The embryo is straight, and in bulk bears about the same relation to the endosperm as in *Hamamelis*.

#### SUMMARY AND CONCLUSION.

1. In *Hamamelis* the anthers have two microsporangia from the beginning.
2. The generative cell in the pollen grain has a cell wall developed which is afterward dissolved.
3. The pollen tube when grown artificially shows a marked tendency to form cellulose plugs, and also forms spheres into which the contents of the tube are withdrawn. Thus far these phenomena have not been observed in normal growth.
4. The development of the pollen tube in the style may be divided into three periods: first period of growth, hibernation, and second period of growth. During hibernation the walls are thickened and the diameter of the tube enlarged, in the next stage having a smaller size and thinner walls.
5. There are several macrospores developed, only one of which becomes functional. It is deeply buried in the nucellus by the growth of tapetal tissue.
6. The germinating macrospore is nourished through a strand of conductive tissue from the chalaza.
7. The antipodals are sunk in the tapering lower end of the embryo sac. This tip is surrounded by deeply staining tissue which for a time resists the dissolving action of the endosperm.

8. The epidermis of the nucellus is the only part not used up by the endosperm. Its walls are thickened and it helps to form the inner seed coat.

9. Fertilization takes place in May, five to seven months after pollination.

10. The embryo is slow to begin growth and has a short suspensor.

11. The seeds sprout normally after lying on the ground for two winters.

12. The hairs serve a twofold function while young, to keep the growing tissues moist, and when mature to keep off moisture.

13. One case of the regeneration of the fibrous layer of the anther wall by the epidermal layer was observed.

14. The other investigated genera of the family all have a resting stage of the pollen, although it is much shorter.

15. The other genera of the family all have anthers with four microsporangia.

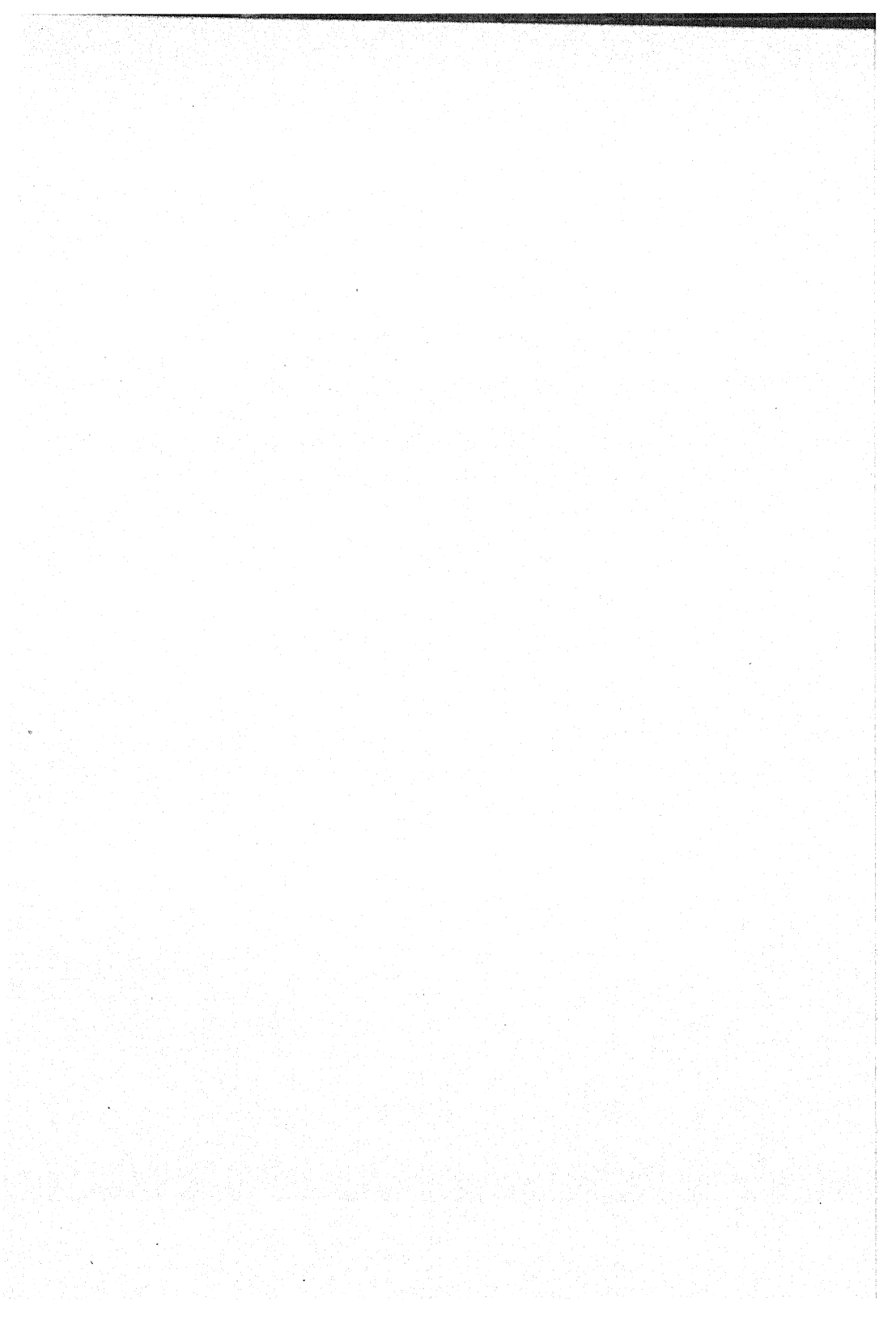
In comparing *Hamamelis virginiana* with its relatives, it seems certain that it was once a spring-flowering plant, whose blossoming has worked backward through the winter. It differs from *H. arborea* essentially in the way its pollen passes the winter, for the development of each is much the same in October.

Most of the plants showing long resting periods in pollen growth belong low in the system, in the Amentiferae; but with the exception of some oaks *Hamamelis* has the longest resting period known. It seems probable, therefore, that this resting period can not be regarded as a primitive character in any case.

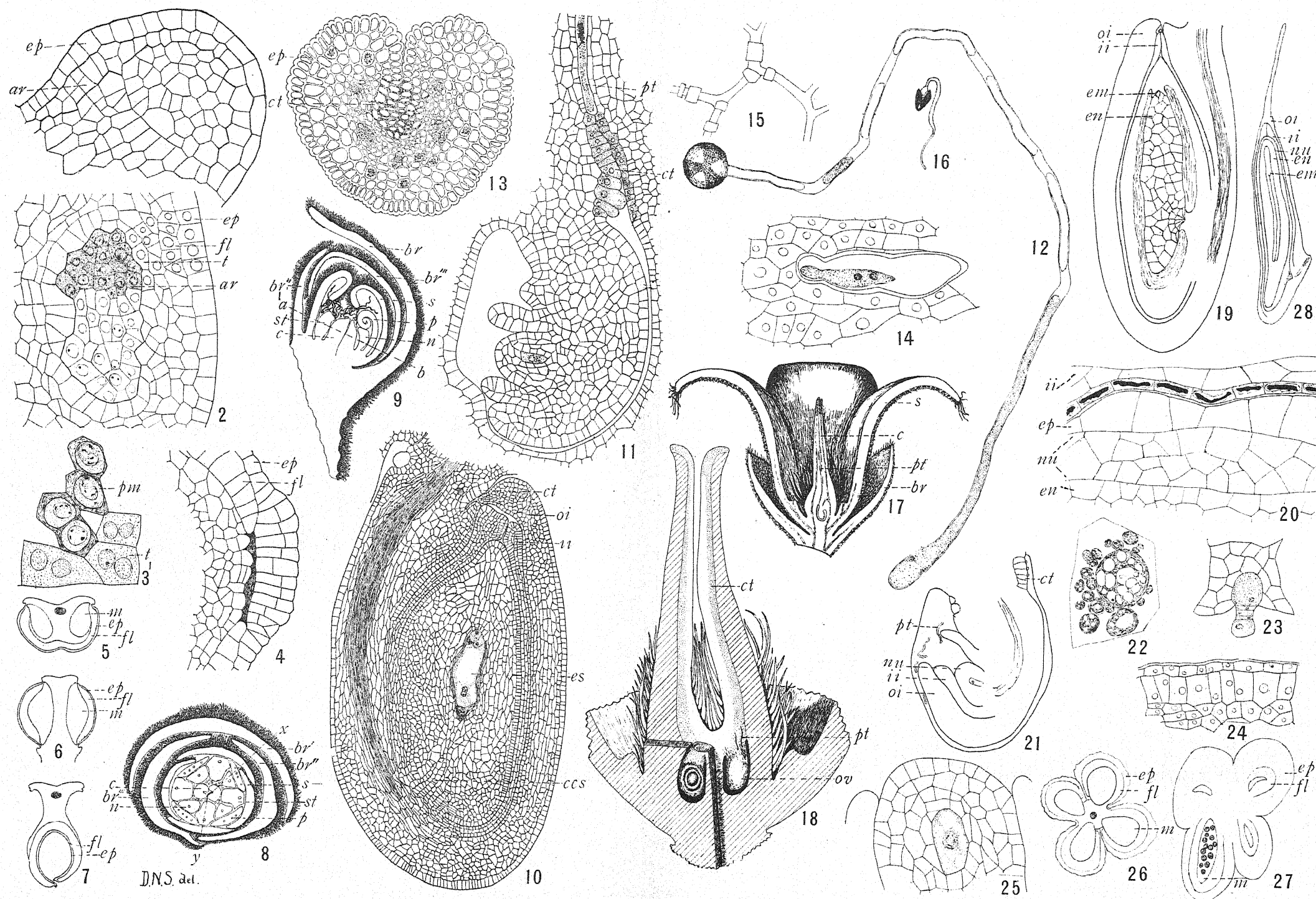
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Waco, Texas.

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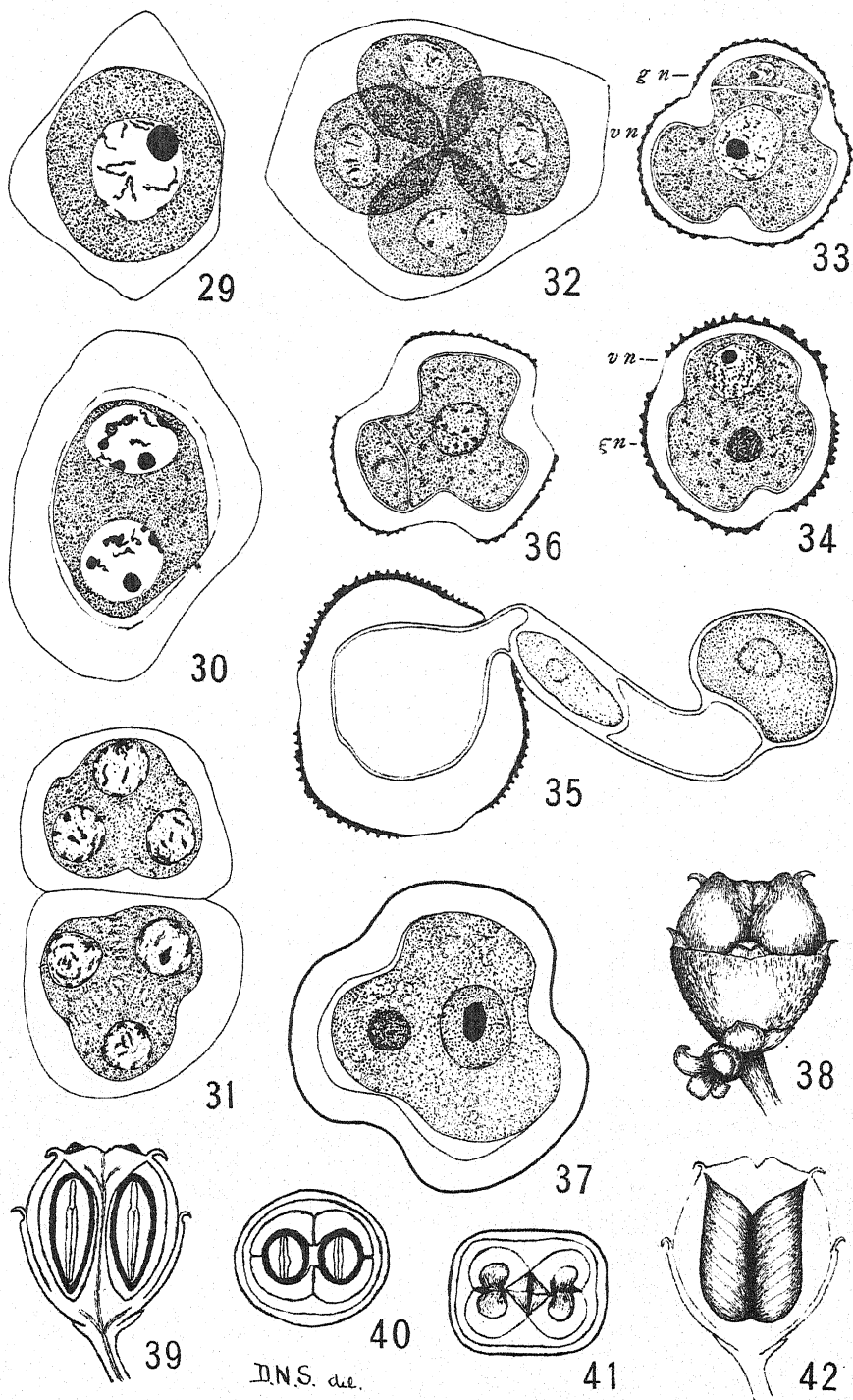
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#### EXPLANATION OF PLATES VI AND VII.

All figures were drawn with a Zeiss camera lucida, and are of *Hamamelis virginiana* unless otherwise stated. The magnifications indicated are those of the reduced plates; those of *Plate VI* having been reduced one-half, and those of *Plate VII* one-fifth. The abbreviations are as follows. *ar*, archesporium; *br*<sup>1</sup>, *br*<sup>2</sup>, *br*<sup>3</sup>, first, second, and third bracts; *c*, carpels; *ccs*, chalazal conducting strand; *ct*, conductive tissue; *em*, embryo; *en*, endosperm; *ep*, epidermis; *es*, embryo sac; *f*, funiculus; *fl*, fibrous layer; *gn*, generative nucleus; *ii*, inner integument; *m*, microsporangium; *n*, nectaries; *nu*, nucellus; *ol*, outer integument; *ov*, ovules; *p*, petals; *pm*, pollen mother-cells; *pt*, pollen tube; *s*, sepals; *st*, stamens; *t*, tapetum; *vb*, vascular bundle; *vn*, vegetative nucleus.

FIG. 1. Growing stamen; longitudinal section. × 550.

FIG. 2. Growing stamen; transverse section. × 550.

FIG. 3. Tapetum and pollen mother-cells. × 550.

FIG. 4. Anther wall showing regeneration. × 220.

FIG. 5. Mature anther; diagrammatic transverse section. × 35.

FIG. 6. Mature anther; diagrammatic longitudinal section. × 35.

FIG. 7. Mature anther, open; diagrammatic transverse section. × 35.



- FIG. 8. Growing flower bud; transverse section in plane *ab* in fig. 9.  $\times 22$ .  
FIG. 9. Growing flower bud; longitudinal section along line *xy* in fig. 8.  
 $\times 22$ .  
FIG. 10. Ovule; longitudinal section.  $\times 97$ .  
FIG. 11. Ovule at beginning of winter.  $\times 220$ .  
FIG. 12. Pollen tube with cellulose plugs, grown in gelatin.  $\times 330$ .  
FIG. 13. Style; transverse section.  $\times 220$ .  
FIG. 14. Hibernating pollen tube.  $\times 550$ .  
FIG. 15. Endosperm cell walls with crystals.  $\times 550$ .  
FIG. 16. Seedling in seed coats.  $\times 1$ .  
FIG. 17. Flower in winter; longitudinal section.  $\times 9$ .  
FIG. 18. Carpels in winter; diagrammatic longitudinal section.  $\times 20$ .  
FIG. 19. Ovule; longitudinal sections.  $\times 35$ .  
FIG. 20. Seed coats.  $\times 175$ .  
FIG. 21. Ovule in spring; longitudinal section.  $\times 80$ .  
FIG. 22. Endosperm cell stored with food.  $\times 550$ .  
FIG. 23. Embryo and suspensor.  $\times 550$ .  
FIG. 24. Cotyledon in seed.  $\times 220$ .  
FIG. 25. Nucellus of *Corylopsis pauciflora* in spring.  $\times 550$ .  
FIG. 26. Mature anther of *Liquidambar styraciflua*; transverse section.  
 $\times 35$ .  
FIG. 27. Nectary of the same; transverse section.  $\times 35$ .  
FIG. 28. Seed of the same, nearly mature.  $\times 5$ .  
FIG. 29. Pollen mother-cell.  $\times 1745$ .  
FIG. 30. First division of pollen mother-cell.  $\times 1745$ .  
FIG. 31. Second division of pollen mother-cells.  $\times 1745$ .  
FIG. 32. Pollen grain, in pollen mother-cell.  $\times 1745$ .  
FIG. 33. Pollen grain.  $\times 1745$ .  
FIG. 34. Pollen grain.  $\times 1745$ .  
FIG. 35. Pollen grain sprouted in gelatin.  $\times 1745$ .  
FIG. 36. Pollen grain, winter condition; *Hamamelis arborea*.  $\times 1745$ .  
FIG. 37. Pollen grain, winter condition; *Corylopsis pauciflora*.  $\times 1745$ .  
FIG. 38. Ripe fruit.  $\times 1.6$ .  
FIG. 39. Fruit; longitudinal section.  $\times 1.6$ .  
FIG. 40. Fruit; transverse section.  $\times 1.6$ .  
FIG. 41. Fruit, after discharge of seed; transverse section.  $\times 1.6$ .  
FIG. 42. Opening layer of capsule; side view.  $\times 1.6$ .

## SEXUAL REPRODUCTION IN THE RUSTS.

A. H. CHRISTMAN.

(WITH PLATE VIII)

THE nature of the aecidium has remained one of the most vexed questions in mycology. BLACKMAN'S<sup>1</sup> recent discovery goes far toward clearing up the most important points and my own results, described below, confirm his general conclusions, though showing a widely different method of conjugation. The literature relating to sexuality and the general cell processes in the rusts has been so thoroughly and justly reviewed and critically estimated by BLACKMAN that I need hardly devote further space to it here.

My studies on the winter conditions of the rusts and the nature of the aecidium led me to the preparation of material for cytological study, and in the spring of 1904 Professor J. C. ARTHUR proposed to Professor HARPER to furnish material from his cultures for cytological investigation. This material was turned over to me. It consisted of a quantity of carefully identified aecidia of several rusts, and since our knowledge of the method of origin of the binucleated condition found in the aecidiospores was at that time entirely lacking as to the details of the behavior of both cells and nuclei, my study was directed largely toward that point.

It was soon found that aecidia of the caeoma type, with unlimited growth, were by far the most favorable material. This type of development apparently admits of less crowding of the hyphae, and as a result the cells and their relations can be made out more easily. Two forms were further found especially favorable because of the large size of their cells and nuclei. These were *Caeoma nitens* S. growing on *Rubus* cult., and *Phragmidium speciosum* Fr. on *Rosa humilis*.

The best fixation was secured by the use of Flemming's fixing solutions; both the strong and weak were very satisfactory. Fixing solutions were sent to Professor ARTHUR and the specimens were

<sup>1</sup> BLACKMAN, V. H., On the fertilization, alternation of generations, and general cytology of the Uredineae. *Annals of Botany* 18:323-373. pls. 21-24. 1904.

put into them by him at Lafayette, Indiana, and mailed at once to Madison. The usual time for fixation was from two to three days. Flemming's triple stain gave the best results. Good preparations were also obtained by the use of Heidenhain's haematoxylin.

In the case of *Phragmidium*, material was found of all ages, so that the entire history from the uninucleated mycelial cells to the fully formed binucleated spores could be easily followed. It was found that in the young pustule the hyphae form a layer just beneath the epidermal cells (*fig. 1*). This layer, in which the direction of the individual hyphae is almost lost, is usually from one to three cells thick. The mycelial cells here are much thicker and shorter than those found in the vegetative hyphae. Each cell has a very dense, finely granular cytoplasm and a single large nucleus. The nucleus occupies a central position in the cell. There is a well-defined nuclear membrane and one large nucleole. The chromatin is always more or less massed at this stage, making a ragged net with the strands very irregular in thickness. Thus a great deal of clear space is left in the nucleus, which is filled with nuclear sap. The chromatin is regularly stained by the violet of the triple stain and the nucleole stains a deep red.

Certain cells now become elongated in a direction perpendicular to the epidermis, forming a continuous series and raising the epidermis (*fig. 2*). The exact origin of the cells of this series is hard to determine; many of them can be seen to be end cells of short hyphal branches. In thick sections, long branches may often be traced between the subepidermal cells of the host, which terminate in one of these cells. In the caeoma the cells are not crowded; there is even considerable intercellular space. Very often it may be seen that cells standing side by side arise from different hyphal branches, or at least from distant parts of the same hypha (*fig. 2, a and b*).

The single nucleus of the cell now apparently divides and the cell elongates into a rather narrower upper part which is cut off as a small distal cell from the larger basal cell. The cell division is very unequal. The end cell as a result is only about one-third the size of the cell beneath it (*fig. 3*). The protoplasm of the end cell is at first dense and appears quite normal. It soon becomes very vacuolar, however, and finally appears quite clear, with only a few strands of



granular material, and the whole cell dwindles in size. The chromatin of the nucleus seems never to have passed into the resting condition, but lies in dense masses, apparently as it was left on reaching the poles of the spindle in the nuclear division preceding. The whole nucleus is very small compared with the nucleus of the larger cell beneath and contains little space between the chromatin masses. The material of the nucleus begins to disorganize and soon becomes a homogeneous mass, which stains a hazy red with the triple stain.

The cell beneath this terminal cell, on the other hand, begins to enlarge, bulging at the middle, and becomes irregularly barrel-shaped. The cytoplasm is dense with small vacuoles. The nucleus enlarges greatly and the chromatin matter is distributed through its interior, forming a ragged network. There is a large, well-defined nucleole.

We have thus a series of oblong cells standing vertically side by side but not much crowded. If we study a series from the margin of a sorus to its center, we find gradually more advanced stages, so that very many conditions of development may often be found in a single section.

Up to this time in the history, the writer's observations agree very closely with those of BLACKMAN. The subsequent behavior of the larger cells, however, which BLACKMAN terms the fertile cells, is very different. Many times two can be found which incline toward each other, coming in contact in a region on their adjacent walls. At this period the remains of the degenerating sterile cells may often still be seen (*fig. 4*). At the point of contact an opening is formed by solution of the cell wall and thus the protoplasts are brought into contact. The pore is small at first, leaving the bases of the gametes quite independent, and often the two tips of the gametes are also separate, as is indicated by the notch at the apex of the conjugated cells (*fig. 5*). By gradual enlargement of the pore the upper halves of the protoplasts of the gametes unite to form a continuous cell mass which still shows plainly the two distinct bases (*fig. 6*). The nuclei, which before fusion occupied a central position in the fertile cells, now come to lie in their upper portions; consequently the two nuclei are brought side by side in the conjugated region. Simultaneous division now takes place. Two spindles are formed which lie side by side in about

the position in which the pore first appeared (*fig. 7*). The spindles in this division are more distinct and not quite so parallel as in subsequent conjugate divisions. Each shows a few short polar rays and to each pole are drawn several (certainly more than two, though the number was not determined) distinct chromosomes. The two nucleoli are at this time lying in the cytoplasm outside the spindle figures. They are less dense than at earlier stages and appear to be disintegrating. Two of the daughter nuclei, one from each spindle, wander back into the bases of their respective cells. The other two remain lying side by side and move into the distal end of the fused portion of the gametes, which now enlarges and elongates (*fig. 8*). A cell wall now cuts off the distal portion of this region, which contains the upper pair of nuclei, and thus the first aecidiospore mother-cell is formed (*fig. 9*). This cell, as has been described frequently, at once divides into two unequal cells, the aecidiospore and the small intercalary cell.

After one spore has been formed, the nuclei in the bases of the fused gametes again move upward into the conjugated portion, which has meanwhile grown in length, and the process of division is repeated. In this way a single row of aecidiospores is formed from each pair of the gametes (*fig. 10*). During these processes the cytoplasm retains the same granular appearance. The nuclei, excepting in figures showing division, always have the same general structure.

From the fact that the bases of the conjugating cells diverge widely, it is suggested that the conditions shown in *fig. 6* might be produced by the bending of a single hypha, as is the case in the development of an ascus. The earlier development of the gametes, however, shows conclusively that nothing of the sort occurs here, and that the cells which fuse may belong to distinct hyphal branches.

We find thus a typical case of the fusion of gametes at the base of each row of aecidiospores, with the difference that the nuclei do not fuse and the cell produced by the fusion germinates at once. The subsequent history of *Phragmidium* has been well worked out and I shall not take it up here.

My material of *Caeoma nitens* did not afford so complete a series of stages, but I have been able to trace with perfect certainty the history as far as the formation of the fertile and sterile cells. As in

Phragmidium, hyphae made up of large dense cells collect in layers one to four cells deep just beneath the epidermis of the host (*fig. 11*). From these hyphae a series of large elongated cells is formed which raise the epidermis. A cell wall cuts each of these cells into a sterile cell and the gamete (*fig. 12*).

The remainder of my material of *Caeoma* was so far advanced in development that each pair of gametes had already formed a considerable series of spores. Here, as in *Phragmidium*, a most conspicuous structure through all the later stages of the development of the aecidium is the basal remnant of the walls which separate the two gametes (see *figs. 6-10*). There may be more or less of it according to the completeness with which the adjacent walls were dissolved away when conjugation occurred, but in all cases it and the two distinct bases remain throughout as an evidence of the double origin of each row of aecidiospores (*fig. 10*).

Modifications of *figs. 6-10* sometimes occur when two gametes lie, before fusion, with the entire length of their adjacent walls in contact. A very complete destruction of the walls in the formation of the conjugation pore now may cause the two separate bases of the gametes almost to disappear. A section of *fig. 8*, showing a lateral or edge view, would appear as a single large cell containing two nuclei. Either of these conditions gives us a figure which might readily be mistaken for a binucleated basidium.

In *Uromyces Caladii* Pers. a further interesting modification was observed. In this form the fused portion of the gametes elongates greatly and the two nuclei come to lie in the upper part of this region. Much of the base of this region, and the two basal parts of the gametes, are occupied by a large vacuole (*fig. 13*). By normal conjugate division of the nuclei followed by cell division, an aecidiospore mother-cell is formed. The fused portion of the cell is so long and the base is so difficult to trace on account of the vacuole that this also may be readily mistaken for an ordinary binucleated cell.

BLACKMAN considers the process described by him for *Phragmidium violaceum* as a "vegetative fertilization," in which an egg—the fertile cell—is fertilized by a vegetative nucleus, and his conclusions seem justified by the nature of the process in *Phragmidium violaceum*. In *P. speciosum* and *Caeoma nitens*, however, the cells

which fuse are apparently equal gametes. If we consider the matter simply from this standpoint, the whole sorus must be considered as a collection of such pairs of equal gametes. The fusion of each pair should form a zygospore like that of the lower molds. There are, however, two important differences. The product of the fusion in the aecidium is a temporary structure which germinates at once, and further, in germinating it produces a considerable number of spores, the aecidiospores, while in the mold normally only one zygospore is produced. If it is found that the same method of fusion occurs in *Micropuccinia* this form might be considered an intermediate stage between the molds and *Eupuccinia*.

Further, it seems plain that each pair of gametes with the spores produced by them constitutes an individual structure. The aecidium cup, which has so often been considered the individual fruit body on account of its likeness to the cystocarp or pyrenocarp, is shown, by the discoveries described above, as well as by those of BLACKMAN, to be a complex of coordinate units rather than itself a morphological unit. An ascocarp is the product of the fusion of a single pair of gametes, while the aecidium arises from a collection of many such fusing pairs. Further, the peridium of an aecidium cup is not to be compared to the perithecial wall of the ascocarp, since it is composed of rows of cells which are morphologically equivalent to the aecidiospores. The tissue protecting the asci, on the other hand, is produced by the massing together of vegetative filaments which do not arise from the fertilized egg.

I am convinced that the method of conjugation above described will be found in the forms with the limited cup as well as in the more indefinite aecidial sori of *Caeoma*. Considering the aecidium a collection of individuals, it would seem that those forms having a peridium are to be regarded as the more highly specialized, while the *caeoma* is the more primitive type.

Against these views, which seem to me the obvious conclusions to be drawn from my discoveries, it may be urged that the spermogonia with their spermatia, showing as BLACKMAN points out very many resemblances to the male cells of the lichens and the red algae, are still left unexplained, and it must be admitted that there is ground for BLACKMAN'S suggestion of the origin of the rusts from the red algae.

RICHARDS'<sup>2</sup> observations of acarpogonial branch in the young aecidium of *U. Caladii* and other forms favor this view. It is quite possible that the gametes in *U. Caladii* are borne on branches arising from such a carpogonium. The final settlement of these questions of affinity must await the study of further forms of the rusts and related fungi. It is especially important, as suggested above, that the nuclear phenomena in species of rust with an abridged life cycle be determined. There can be no doubt that the proof given above of the existence of a sexual fusion of gametes in the aecidium finally disposes of the conception of DANGEARD<sup>3</sup> and SAPPIN-TROUFFY<sup>4</sup> that the teleutospore is an egg, and the nuclear fusion which occurs in it the equivalent of the sexual fusions elsewhere among the algae and fungi. On the other hand, these discoveries also confirm and give new significance to the conceptions, so clearly set forth by ARTHUR,<sup>5</sup> that the aecidium represents the stage of sexual rejuvenescence. There can be no question that BLACKMAN is in general correct in the contention that the nuclear phenomena in the teleutospore are concerned with chromosome reduction and mark the close of a sporophyte generation which began with the cell fusion in the aecidium. Here again, we need further facts as to the rusts with reduced life cycle before the doctrine of an alternation of generations, such as BLACKMAN maintains, can be regarded as finally established.

MAIRE'S<sup>6</sup> conception that the nuclear fusion in the teleutospore is a *mixie*, was developed on the basis of the belief that no real cell fusion occurs in the life cycle of the rusts. It is at least a fair presumption that while no nuclear fusion occurs in the aecidium, the fusion of gamete cells described above presents all the essential

<sup>2</sup> RICHARDS, H. M., On some points in the development of the aecidia. Proc. Amer. Acad. 31:255-270. *pl. I.* 1896.

<sup>3</sup> DANGEARD, P. A., La reproduction sexuelle des champignons. Le Botaniste, 7:89-130. 1900.

<sup>4</sup> SAPPIN-TROUFFY, M., Recherches histologiques sur la famille des Urédinées. Le Botaniste 5:59-244. *figs. 69.* 1896-97.

<sup>5</sup> ARTHUR, J. C., The aecidium as a device to restore vigor to the fungus. Proc. Soc. Promotion Agric. Sci., 23d annual meeting.

<sup>6</sup> MAIRE, R., Recherches cytologiques et taxonomiques sur les Basidiomycetes. 1902.

features of sexual conjugations as found in other plants and animals. Superficially considered, RACIBORSKI'S<sup>7</sup> conception that the sexual union may be regarded as consisting of two phases, cell fusion and nuclear fusion, might seem to fit the conditions found in the rusts. I am inclined, however, to accept BLACKMAN'S conclusion that the fusion in the teleutospore has wholly to do with the reduction of the number of chromosomes.

The difference between the method of conjugation in *P. violaceum* as described by BLACKMAN and *P. speciosum* as I have described it above indicates the necessity for a comparative study of a large number of aecidia to determine the nature of the sexual process in the group as a whole. There can be no question, however, that with the discoveries already made the existence of true sexual cell fusions in the rusts is finally established.

The writer feels greatly indebted to Professor ARTHUR for the careful selection and fixation of the material used in this work, and to Professor HARPER for valuable suggestions and kindly assistance in many ways.

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#### EXPLANATION OF PLATE VIII.

The figures were drawn with the camera lucida. Figs. 1, 2, 10, 11, and 12 were drawn using the Bausch & Lomb 1-inch eyepiece and  $\frac{1}{12}$  oil objective; all others were drawn with  $\frac{1}{2}$ -inch eyepiece and  $\frac{1}{12}$  objective, the tube length in either case being 185<sup>mm</sup>.

#### *Phragmidium speciosum*.

FIG. 1. Hyphae massing beneath the epidermis in the early stages of the caecoma.

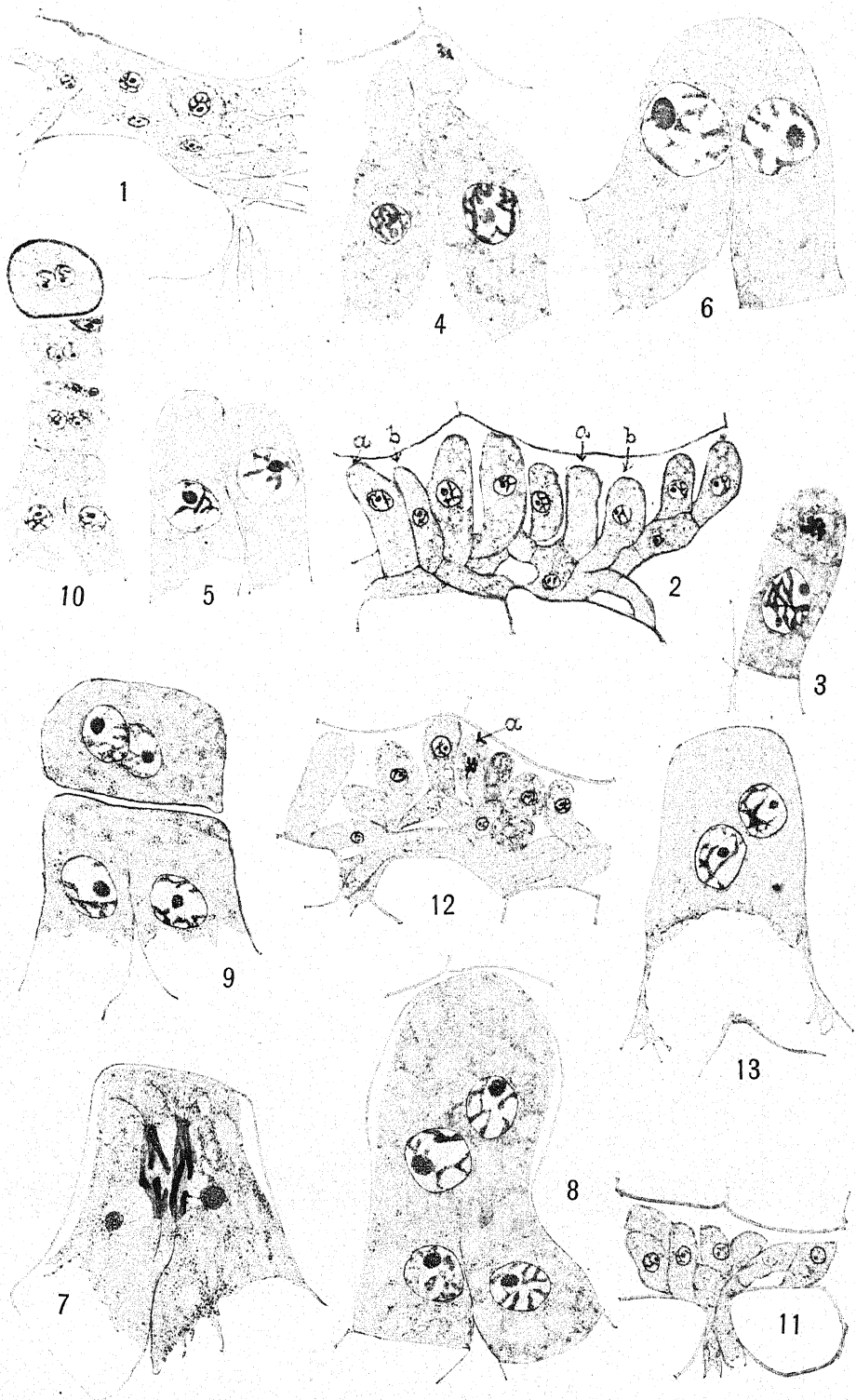
FIG. 2. The series of large cells formed preparatory to division into sterile cell and gamete; *a* and *b*, cells lying close together, which appear to be parts of different hyphal branches.

FIG. 3. A cell of such a series as is shown in fig. 2 after the division into the smaller sterile cell and the large gamete.

FIG. 4. Two gametes about to fuse; sterile cells remain though very much reduced in size.

FIG. 5. Fusing cells with the small conjugation pore just formed.

<sup>7</sup> RACIBORSKI M., Über den Einfluss äusserer Bedingungen auf die Wachstumsweise des *Basidiobolus ranarum*. Flora 82:107-132. figs. 11. 1896.



CHRISTMAN on RUSTS







FIG. 6. Same as fig. 5, slightly more advanced; the nuclei lie nearer the distal end than in earlier stages.

FIG. 7. Simultaneous nuclear division following the fusion.

FIG. 8. A stage following nuclear division in which the fused mass contains four nuclei, two side by side in the distal end and one in each of the bases.

FIG. 9. The aecidiospore mother-cell formed by a cell wall cutting off the upper portion of the protoplast.

FIG. 10. A figure taken from a thick section showing several aecidiospores, intercalary cells, and the two gametes at the base; the remnant of the basal part of the dividing wall being evident between the two gametes.

*Caecoma nitens.*

FIG. 11. Hyphae of rust massing beneath the epidermis in very young sorus.

FIG. 12. Series of large upright cells; *a*, a nuclear division preceding the throwing off of the sterile cell.

*Uromyces Caladii.*

FIG. 13. A pair of gametes fused, showing the nuclei in the upper portion of the protoplast, the large vacuole in the lower part, and the two less conspicuous bases.

THE FORESTS OF THE FLATHEAD VALLEY, MONTANA.  
CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY.  
LXVII.

HARRY N. WHITFORD.

(WITH MAP AND TWENTY-THREE FIGURES)

[Concluded from p. 218]

THE undergrowth of the Douglas spruce-bull pine combination is decidedly heath- or prairie-like. In the more open places grass is predominant, and associated with the grasses are *Balsamorhiza sagittata*, *Monarda scabra*, *Lupinus ornatus*, and *Clarkia pulchella*. The most common bushes are *Prunus demissa*, *Amelanchier alnifolia*, *Opulaster pauciflorus*, and *Symphoricarpos* sp. In places where the rock is near the surface a heath-like appearance is given to the undergrowth by the presence of *Cladonia* sp., *Arctostaphylos Uva-ursi*, *Campanula rotundifolia*, *Selaginella densa*, *Lepargyrea argentea*, and *Pteridium aquilinum*; other forms noted were *Galium boreale*, *Achillea millefolium*, *Holodiscus ariaefolia*, and *Populus tremuloides*; and along the pebbly shores of the lake Crataegus is very characteristic.

On the southern slope of Swan Hill the vegetation conditions found on the exposed slopes of Mission Mountains are approximated, though this area is slightly more mesophytic; and the same may be said for the east side of Swan Lake. Here the shores end abruptly in a range of hills on whose west slope Douglas spruce and bull pine are characteristic, though here and there are scattered groups of western larch. Another meso-xerophytic area on the east side of Big Fork River, not far from the foot of the lake (*map*), has already been mentioned.

The country lying to the south and southwest of Flathead Lake is semi-arid (*fig. 5*), but in favorable situations there is some woody vegetation. A fringe of trees around the borders of the lake contains principally Rocky Mountain juniper, hawthorn, and bull pine; and the same condition is found along Pend d'Oreille River where

a low terrace has been formed. Dry ravines extending back from this lake also have a woody vegetation. The difficulties which trees meet in getting a start in a prairie region should be recognized. A very large majority of the seeds never germinate, and many that do germinate dry out before they have made a good start; and the sod also in many instances prevents the seeds from reaching the soil. The head of a ravine works back during freshets, undermines the prairie sod, and thus disturbs the vegetative equilibrium that had been established, offering a place more or less free from competition. If seeds fall on one of these bare places and do not dry out before the next rain which disturbs more of the soil, they may be buried by the moving soil; the seeds thus having the advantage of being planted and supplied with moisture at the same time. If the conditions remain stable long enough for the plant thus started to establish itself, it may hold its own even though there is considerable movement of the soil in the erosive process. Of course only a few plants out of the number thus established can exist long in the severe conditions of drouth that prevail in these regions.

The large moraine at the foot of the lake is almost destitute of trees (*fig. 5*), but isolated trees of Douglas spruce and bull pine were observed on its northern slope, and around them were a large number of seedlings, nearly all of which, in spite of their needle-like leaves, were nipped off by the cattle. It is very possible that if it were not for the cattle more of the trees would reach maturity, though it is doubtful if the increase would be very appreciable. However, if a slope was slightly more protected from the drying winds and the cattle did not interfere, open stands of both Douglas spruce and bull pine might exist. The hillside near the region shown in *fig. 6* illustrates the point; it slopes to the north, and the part of it under discussion is too high up the cañon of the Pend d'Oreille River to be influenced by proximity to the river, though probably trees near the river are the source of supply for the seeds that stocked the hillsides higher up. The bank is too steep for cattle to maintain a foothold easily, and except along paths young trees are not eaten by them.

As one approaches the forest formation to the north and east from the south end of Flathead Lake, trees become more prevalent, a number of hilly islands (*fig. 5*) in the lake showing an interesting

series of gradations. First there are hills with bull pine and a few Douglas spruce on the north and east slopes and few or none on the exposed slopes; then there are hills where a considerable number of bull pines find favorable conditions for development on the exposed sides of the hill (*fig. 18*), and with these there is some Douglas spruce. On the protected slopes the Douglas spruce becomes more abundant and may even destroy new growths of bull pine by their shade. Another set of hills nearer the forest formations show the south slopes fairly well covered with bull pine and Douglas spruce, while the bull pine has become less abundant on the protected slopes where the western larch element has been introduced. Thus there are all gradations from hills with few or no trees to those that have mesophytic elements on the north slopes. Of course there are many variations; for instance, hills a little to the north of west of the town of Big Fork have their southern slopes almost destitute of trees, while the protected slopes have a stand of Douglas spruce, western larch, and some bull pines. The series may be carried still further. It has been shown that the west slope of Mission Mountains has a forest of Douglas spruce and bull pine, while on the protected slope western larch is the most prevalent, and with it trees like lowland fir, silver pine, and giant arborvitae, which require still more moisture, are found. If the rainfall be sufficient, a mesophytic forest may be found on the exposed as well as on the protected slopes.

It may be well to analyze the conditions that make the so-called protected slopes more desirable for trees. Of course the great factor that prevents tree growth is the lack of moisture. If an annual rainfall of 400<sup>mm</sup> falls upon a hill similar to those just described, and in gentle showers so that there will be little or no run-off, the water that leaves the soil directly must do so by evaporation, the remainder soaking in and becoming available for absorption. It is obvious that the slopes receiving the strongest insolation and exposed to drying winds will lose the most water by evaporation, and these are the south and west slopes; hence the north and east slopes will have more moisture in the soil. Again, the plants growing on these protected slopes do not receive so much heat and are not exposed to the drying winds, hence do not lose so much water by transpiration; they not only get more moisture but do not need so much to supply

the transpiration streams, therefore trees that require better moisture conditions can exist in these situations.

The silvicultural habits of Douglas spruce and bull pine remain to be summarized. Douglas spruce has the widest life range of any of the species found in Flathead valley, being found at higher altitudes than any other of the lowland species, with the exception of



FIG. 18.—View of a portion of an island near the south end of Flathead Lake; a park-like growth of bull pine and Douglas spruce is present.

Engelmann spruce. It is found accompanying western larch all through the mesophytic forests of Swan valley, and forms even a greater percentage of the trees in the meso-xerophytic regions, and advances into the prairie sometimes as far as bull pine. However, this power of adaptation is not without an effect upon its form, for in high altitudes and on the border of the prairie region it is dwarfed and sometimes fasciated. In mesophytic conditions it reaches the dimensions of the trees with which it is associated, and even these

trees, though larger than most of the conifers of the eastern states, are small compared with the vigorous trees found in the hemlock-arborvitae-Douglas spruce forests west of the Cascade Mountains. It is in this region of greater rainfall and warmer winter months that Douglas spruce makes its best growth. With its great power of adapting itself to adverse conditions, it has spread through all the Rocky Mountain region as far south as Mexico. While Douglas spruce can adapt itself to varying conditions of moisture, it is very intolerant of shade, in this respect being like western larch, and even requiring slightly more open places in the forest to gain a foothold. Thus the tree will be reproduced only in open places in the forest.

The distribution of bull pine in Flathead valley is more limited than that of either Douglas spruce or western larch. It occurs in open park-like growths on the borders of the prairie formation, with patches of the prairie between (*fig. 18*). In the forest formations in the vicinity of Nigger Prairie there is a close stand of this species (*fig. 14*). Indeed so thick are the trees in certain situations that there is not sufficient light under them for the reproduction of either Douglas spruce or western larch, though young trees of Engelmann spruce and lowland fir can endure the shade. Isolated groups of bull pine are scattered through Swan valley, usually along streams where abundant light can reach them, and in pebbly soils, where other trees have difficulty in maintaining a stand, bull pine is found. Wherever a single tree is found surrounded by other trees it usually overtops them, showing that it probably started before they were present, for it is exceedingly intolerant of shade; it must have open places in which to pass its young stages, and this perhaps accounts for its scarcity in the mesophytic area in deep rich soils. Where found in Swan valley, it is a very healthy tree and very likely would do well in pure stands there if given a chance. In other words, bull pine does not grow in the dry soils on the border of the prairie because it prefers the moisture conditions found there, for it does better in the soils where there is more moisture; it is almost entirely forced out of the latter soils in the struggle for existence with the more successful trees. It undoubtedly demands a greater amount of heat than the other species, with the possible exception of lowland fir, for its altitudinal range is more limited. The highest point at which it was observed on the surrounding mountains was 1375<sup>m</sup>.

A summary of the relation of the prairie to the forest in this region is as follows: (1) there is less moisture in the prairie soil than in the forest soil; (2) this is due primarily to the smaller amount of rainfall; (3) in the prairie formation forests may exist in certain topographic situations, as along streams and other bodies of water, and on protected hill-sides; (4) in the forest formation prairies exist where the character of the soil is such that it will not easily hold water; by the gradual addition of humus such soils may be changed sufficiently in their water-holding capacity to permit more mesophytic conditions and in some instances a climax western larch-Douglas spruce combination.

Objection may be made to the use of the term mesophyte for plants with xerophytic leaves. WARMING classifies all conifers as xerophytes because they grow in dry soils. In the eastern United States in contrast with the broad-leaved deciduous trees the conifers are undoubtedly xerophytes, comparatively speaking. That is, during the summer months the deciduous tree requires more moisture than the conifers, therefore the deciduous tree is excluded from the dry soils. In the northwestern United States the coniferous forests occupy the mesophytic soils almost to the entire exclusion of the deciduous element. As shown in the discussion on the climatic formations, this is due to a peculiar climate in which the summers are comparatively cool and dry, and the winters comparatively warm and excessively wet. In such a climate the deciduous tree is lacking, except in edaphic situations, on account of the cool dry summers, because with its broad transpiring surface it requires more moisture than it is able to get. The narrow-leaved sclerophyllous trees, on the other hand, while they do not necessarily thrive during the dry summer months, because of their reduced transpiring surface they are permitted to exist, while the broad-leaved deciduous trees cannot. During the winter the reverse is the case, for deciduous trees with their bare twigs are better able to endure severe conditions than are the conifers. On the other hand, if the climate is moist and warm, the conifer is able to do a considerable amount of photosynthetic work. Thus the deciduous tree requires more moisture during the summer months and is consequently more mesophytic at that season; on the other hand, the coniferous tree requires more moisture during the winter months and consequently is more mesophytic at that

time than the deciduous tree. Because of the equable distribution of moisture throughout the year in sufficient quantity in the eastern United States both can exist, although the deciduous element is able to occupy the mesophytic areas almost to exclusion of the coniferous element. In the northwestern United States the conifers, because the climate in which they grow is more suited to them, are able to occupy the mesophytic areas, and hence, so far as that climate is concerned, are mesophytes. Although they may have xerophytic leaves, the structure of the tree as a whole is more mesophytic during the non-growing season than is that of the deciduous tree. Taking the entire year into consideration, for the reasons given above I think that I am entirely justified in speaking of conifers as mesophytes.

### III. THE INFLUENCE OF FIRES ON THE PRESENT COMPOSITION OF THE FORESTS OF FLATHEAD VALLEY.

In the discussion of the forest conditions up to this point little attention has been given to the influence of fires. There is scarcely a section of land in the area investigated that has not been more or less burned over. In some places mere surface fires have run through the woods, scorching the trunks of the trees sufficiently to scar them. In other situations the fires have burned vigorously through small areas killing many of the trees. Still other fires have destroyed completely large areas, leaving many acres with not a single tree. Such is the case on the west slope of the Mission Mountains (*figs. 4, 16, 17*). There are many small clearings made by settlers, who after proving up their claims have deserted the cabins erected upon them (*fig. 19*).

By marshaling the facts collected by a study of the conditions of reforestation in these fire clearings, nearly all stages in the establishment of new mature forests were determined. Studies in similar regions outside of the area plotted have proved very helpful in the interpretation of these conditions. Some important principles must be kept in mind in explaining what plants will first get a foothold in the open places made by fires. These are as follows:

1. The subterranean parts of some plants that are able to sprout from roots or underground stems may not be destroyed by fire. The sprouts of these species will give the burn a decided aspect in a short time.



2. Other things being equal, the plants whose seeds are in the burn first will gain the earliest foothold.

3. Those plants that have seeds there early after fires will be those that have seeds well adapted for distribution.

4. Of the plants that have their seeds equally well adapted for distribution, those with seed-bearing representatives standing nearest the burned area will have the advantage.

5. Again, other things being equal, of those species that have their seeds equally well adapted for distribution and have seed-bearers equally near the clearing, the species that produce seeds most abundantly will be apt to win out in the struggle.

6. The species that can resist fires the best are likely to have left standing in or near the area itself seed-bearing parent plants.

7. The conditions of the soil must be such that it will permit the germination of the seeds that fall upon it. If the soil is too moist, too dry, too poor, or too much shaded, no matter how many seeds fall upon it, none will germinate.

These well-known principles will aid in the determination of the causes of the many complex conditions of forest growth after fires. Before the actual conditions of the clearings are considered, however, the ecological habits of another tree, the lodgepole pine, must be known.

The lodgepole pine covers large areas in Swan valley, sometimes forming almost pure stands. It is able to exist and thrive in those moist areas where it has to compete only with the spruce and its associates. It is found mixed with all the other species in the mesophytic portion of the valley. Toward the borders of the meso-xerophytic areas it is not so prevalent, though signs of it were noted west of Echo Lake and in the mesophytic portions of the west slope of the Mission Range. It does not advance into the prairie formation, however, so far as the bull pine and the Douglas spruce. Its altitudinal range was not investigated. It is difficult to tell whether or not this tree would maintain a stand in the Flathead valley if it were not for the influence of fires. It is intolerant of shade, in which respect it may be ranked with western larch and Douglas spruce, reproducing in open places only. No young trees were noted in the shade, save an isolated poorly developed specimen now and then

in the slight shade of a mature stand of the same species. Probably it is a little less exacting in its light requirements than western larch and Douglas spruce.

The lodgepole pine is a prolific seeder, beginning to bear fruit early in life. Out of twenty trees varying in age from five to twenty years, many had cones. The youngest tree noted with cones was six years of age, one at this age having seven cones. On one tree nine years old fifty cones were counted. It was a common thing to find clumps of trees 3 to 4<sup>m</sup> high fruiting abundantly. As will be shown below, this habit of fruiting early in life is of very great advantage to this species. Another thing of very great importance is the fact that the cones remain closed in some instances a number of years, thus preserving the seeds. The heat of a fire will open them and liberate the seeds, many of which will escape injury and germinate at once. The lodgepole pine, during its early stages at least, grows rapidly in height, and this gives it some advantage over its competitors. From the measurements of twenty-five specimens each of lodgepole pine, western larch, and Douglas spruce, the average rapidity of growth in height per year is shown to be as follows: lodgepole pine 52<sup>cm</sup>, western larch 27<sup>cm</sup>, Douglas spruce 20<sup>cm</sup>. Although these averages are from rather meager data, they are sufficient to show that the lodgepole pine has by far the most rapid growth.

In contrast with western larch, Douglas spruce, and bull pine, lodgepole pine has poor fire-resisting qualities. Except in old trees the bark at the base is comparatively thin; the cambium layer is thus easily scorched and killed. In this way many whole forests of trees are destroyed by fires that are not intense enough to consume the trunks. It is not an uncommon thing to see acres of dead standing poles of this species that have thus been swept by fire. In showing how successful lodgepole pine has been in obtaining a foothold in the forests of Swan valley, the principles mentioned above must be kept in mind. The rôle that the plants other than conifers play in the reforestation stages will be treated in another connection. In order that the conditions may be understood more clearly, hypothetical cases will be assumed, and when these hypothetical cases are realized attention will be called to them. Suppose a limited area is burned in the midst of a forest in which western larch and Douglas

spruce are the dominating trees, and that these are mixed with lodgepole pine, silver pine, and lowland fir. Suppose that the trees surrounding this area all bear cones, and all have their seeds equally well adapted for wind distribution. Since not one of the conifers found in the region is able to sprout from the roots that would be protected from the fires, all would have to start from seed. Let us suppose

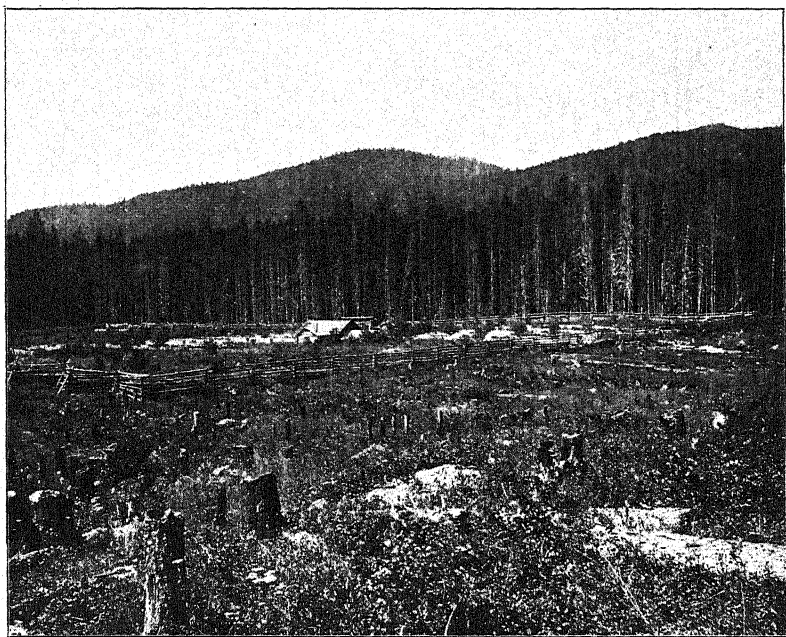


FIG. 19.—A clearing in a lodgepole pine forest in Swan valley; east slopes of Mission Mountains in the background; these slopes have a mesophytic forest of western larch and Douglas spruce.—Photograph by PRAEGER.

that the seeds of all fall in equally favorable places, and that the seedlings that spring up are numerically proportional to the parent trees in the undestroyed stand surrounding the burn. Each species in the forest adjoining the new growth will thus be represented in the burn in the same proportion as it is in the mature stand. If all the young trees grow with equal rapidity, and the natural thinning out is proportionately distributed among the species, the new stand will be just like the old. There are some small burns where this

condition is approximated; of course the proportions are not exactly the same in the old and new stands (*fig. 20*). Granted that any one of the species in the young forest grows more rapidly in its youth than the others, other things being equal it would gain an ascendancy over its neighbors, and in the forest approaching maturity it would have more representatives than in the old forest. As already shown, lodgepole pine bears exactly that relation to Douglas spruce and

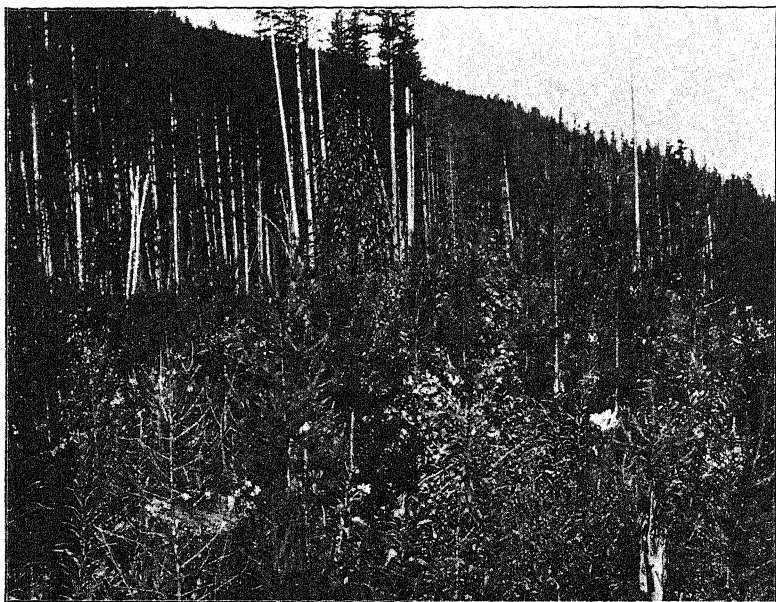


FIG. 20.—Young growth of lodgepole pine and western larch in a clearing surrounded by older trees of the same species, both of which have seed-bearing trees; other plants are dwarf maple and a willow, both of which sprout from old stumps; fireweed is also a characteristic plant.—Photograph by PRAEGER.

western larch at least, and probably to the other species, though no measurements were taken for them. In the new forest thus established, lodgepole pine has made a gain on the other species. However, it reaches maturity sooner than the others, and in the old forest it is the first to drop out in the struggle for existence, so that while in the middle-aged forest it may have had some slight advantage, it loses this and often is entirely eliminated from the mature stand.

Many instances were noted, especially in the region outside the plot mapped, in which lodgepole pine was thus being driven out of forests where doubtless it was more prominent in the young stages of development.

Referring again to the original case, it will be seen to be highly improbable that the species in the stand around the hypothetical burn

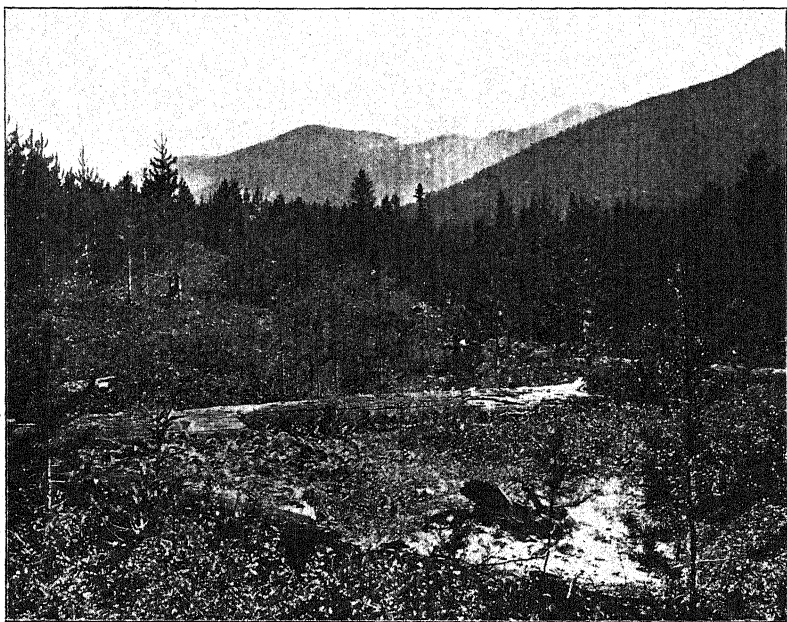


FIG. 21.—Young growth of lodgepole pine and Engelmann spruce in a clearing of the same species.—Photograph by PRAEGER.

would produce seeds equally well. Some species might not have any seeds at all, and they would form no part in the new forest unless a few seeds are blown into the area from regions where there are seed-bearing trees. The lowland fir during the past two years has produced few if any seeds in Swan River valley. Any burn made in the valley then within two years could not be stocked with seeds of this species. If for instance Douglas spruce or western larch produce seeds more abundantly than any of the other trees, they are likely, other things being equal, to have more representatives in the

new forest than in the old. So if any other tree, lodgepole pine for example, has more seeds than the others, it will increase in numbers in the new stand that is formed. So far as its relation to restocking a burn is concerned, a tree that does not produce seeds might just as well not exist at all.

This leads naturally to another modification of the hypothetical case, in which the forests that surround the burn have only one or two species instead of a number. The result will be that these species are likely to be the only ones found in the burn. Such a condition is seen in *fig. 20*, where the forest that surrounds the clearing is composed mostly of western larch and lodgepole pine, and these species are the predominating ones in the new growth. *Fig. 21* shows a clearing surrounded principally by lodgepole pine and Engelmann spruce, which are almost the only trees present in the new stand. Again, *fig. 22* shows that bull pine, western larch, and Douglas spruce are present in an opening in a mature forest of these species. Another explanation for this, however, is that the area is situated on the border of the meso-xerophytic region where probably no other species could exist, even if their seeds were present.

This leads to still another modification of the hypothetical case. Assuming that the seeds of all the species are present, it is highly improbable that they would find equally favorable places for germination. The case just cited (*fig. 22*) is an instance of where all except western larch, Douglas spruce, and bull pine are ruled out. If the fire burnt out an Engelmann spruce stand surrounded by a less swampy region in which Engelmann spruce, lowland fir, silver pine, Douglas spruce, western larch, and lodgepole pine were present, only Engelmann spruce and lodgepole pine would be able to restock it, for these are the only species that could grow in the swampy situations. An instance of such restocking was noted near the head of the bay-like area of meso-hydrophytic forest southwest of Ross Lake.

Still other conditions of reforestation remain to be explained. Taking the hypothetical area that has been restocked with the seedlings of all the trees in the surrounding forest, and assuming that the young growth is approximately fifteen years of age, the only species of this young growth that would have fruit is lodgepole pine. The cones on this pine would be more or less abundant, and on all

the others the cones would be absent. If a fire should sweep through this young growth, destroy it, and at the same time consume some of the original forest around it, thus extending the limits of the original burn, what would be the result? The extent of the burned area being greater, the seeds of the trees bordering it could not so readily be carried to the center of the burn. But this portion of the clearing would be restocked with the seeds of young lodgepole pines that were destroyed by fire, but whose seeds would be more or less protected from the fire by the cones. Some of the cones would be cracked open by the heat of the fire and the seeds would be liberated. The result would be that the next forest would contain more representatives of lodgepole pine than the former forest, and that they would be more numerous in the center. Indeed this center might contain a pure growth of lodgepole pines. Another such fire in the course of fifteen or twenty years or less would enlarge this area at the expense of the other species. Thus almost if not quite pure forests of lodgepole pines of considerable extent would be established. It is very probable that the mature lodgepole pine forest found in Swan River valley was established in this way (*fig. 23*). The evidence for this is as follows:

1. In no case was a stand of this species found in which there were not noted dead and charred trunks of western larch and Douglas spruce, mostly the former; these because of the thick bark would be the last to yield to the fire. In some instances mature live trees of western larch were observed towering above the younger lodgepole pine forest. In these cases there were isolated specimens of young western larch of about equal age growing with lodgepole pines (*fig. 12*).

2. In nearly all cases these forests grade imperceptibly into more mature forests in which the lodgepole pine element is entirely or nearly wanting. The mature forests of western larch, Douglas spruce, silver pine, lowland fir, and lodgepole pine are in many instances growing in soil that is similar in moisture content. Thus it cannot be said that the difference in the two stands is due to the character of soil conditions.

3. In the meso-hydrophytic situations there is often a gradation from a spruce forest to a mixture of Engelmann spruce and lodgepole pine, the latter stand being much younger than the former.

4. In stands that contain little or no signs of fires, the lodgepole pine element is absent or nearly so.

5. Nearly all stages in the development toward this condition were noted. Thus, *fig. 20* shows a comparatively recent clearing in a young lodgepole pine forest, which is in turn surrounded by a mature forest of western larch and Douglas spruce in which the lodgepole pine element is inconspicuous. *Fig. 12* shows an almost pure growth of this young forest with mature trees of western larch in it. In another place there is a more mature growth in which only charred trunks of larch tell the tale.

For the reasons given above, it is believed that the explanation for the lodgepole pine in the area plotted is the correct one. As before stated, observations were not limited to this immediate region, and many instances might be cited where burned areas similar to those described have become reforested with lodgepole pine. It will not be out of place to repeat that the advantage which it has over the other species in the region is due to its capacity to produce seeds early in life, and its habit of retaining the seeds in its cones for a number of years, thus preserving them for a greater or less length of time. In forests partially destroyed by fire the trees of western larch and Douglas spruce, because of the capacity of their trunks to resist rather severe burnings, will restock the burned areas. Fires of this nature, repeated sufficiently often to prevent any young lodgepoles from becoming old enough to produce cones, will militate against the latter, while Douglas spruce and western larch will have cone-bearing trees on the ground so long as the fires are not too intense. As soon as these are destroyed, then the seed supply is cut off and restocking from that source at least will discontinue.

It will be seen readily that if the fires that have made the lodgepole pine condition possible are repeated every five years, for instance, the young growth forests of that tree will not be permitted to follow each other in procession, for the five-year interval between fires will be too short a time to permit lodgepole pine to produce seeds. Then of course all forest growth will be completely destroyed and the area will not become clothed with trees until restocked with seeds from the neighboring undestroyed forests. The further these are away, the longer it will take for seeds to reach the devastated area. However,



if the interval between the fires is sufficiently long to give lodgepole pine time to produce seeds, after each fire a forest of lodgepole pines will spring up to replace the old. Such fires enable lodgepole pine to perpetuate itself so long as the soil is able to furnish the requisite amount of nourishment, but a checking of fires will in time bring about the normal conditions. This has been done about as follows:

The fires being absent, the lodgepole pine stand is permitted to reach maturity. As it does so, seeds of forest trees in the neighboring undestroyed or partially destroyed stands have had time to spread into the lodgepole pine forests. Seedlings of those trees that can tolerate the shade will get a start at once, if the other conditions are favorable. Thus in many instances silver pine, lowland fir, and Engelmann spruce were noted growing under lodgepole pine stands in Swan valley. Also in the Terry Lake region

seedlings of giant arborvitae and western hemlock were observed in similar situations, although, because of the restricted area to which

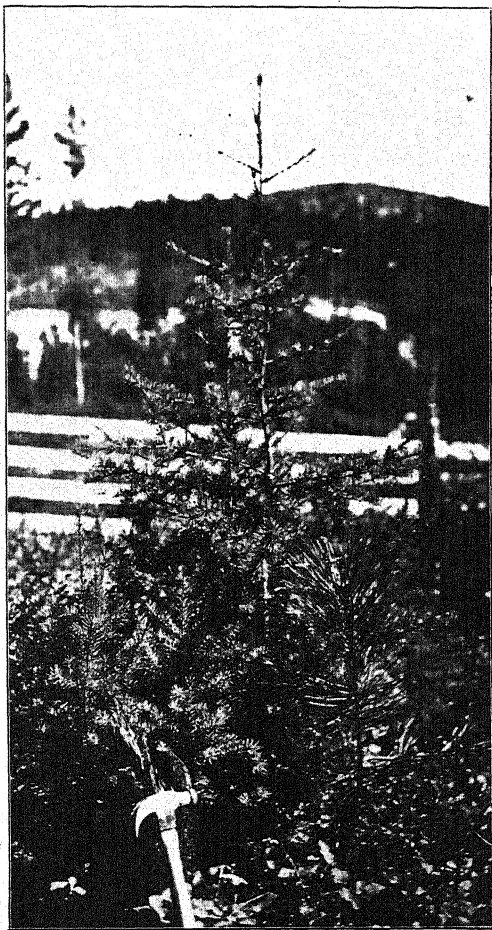


FIG. 22.—Young growth of western larch, Douglas spruce, and bull pine in a clearing of the same species.—Photograph by PRAEGER.

these two species are confined, their occurrence under lodgepole pine stands is not common. As soon as openings are made in the forest of mature lodgepole pines, due to causes other than fires, this undergrowth may spring at once into prominence and may come to occupy a place in the mature forests. At the same time the openings have made it possible for the existence of seedlings of such trees as western larch and Douglas spruce which demand light for germination. Of course lodgepole pine seedlings can germinate here also, and in the first generation or two they will still predominate; but each new generation will have fewer specimens of the latter species, for since it is not a long-lived tree, a canopy of the mature forest of the other species will in the long run crowd it out by density of shade, or reduce its occurrence to isolated trees here and there in the forests. In this way the forests will revert to the normal conditions. The time it will take to do this depends upon the nature of the conditions that the last fire left. If the lodgepole pine conditions had been established for a wide area, the time would be long, perhaps covering many generations of growth. If on the other hand the fire only partially destroyed the original forest, one or a few generations would suffice to permit the re-establishment of a forest similar to the original. Between these two extremes are all stages, some of which have been described. Indeed the present forest formations are a complex expression of the influence of fires upon them.

The general aspect of a lodgepole pine forest approaching maturity is somewhat different from that of other stands. It has already been shown that the growth in height is rapid. In dense stands of young growth the poles are long and spindling, hence the name lodgepole pine. The small diameter of the bole of the tree is very characteristic. A forest in which the average age of the trees is about one hundred years is seen in *fig. 23*. In this forest, where the trees are over a hundred years old, the average diameter is probably 20<sup>cm</sup>, many trees being only 15<sup>cm</sup> in diameter.

Compared with the other forests growing in like situations, the canopy that a lodgepole forest forms is not very heavy. This permits more light to reach the forest floor, hence there is a greater development of undergrowth. It has already been shown that seedlings of silver pine, Engelmann spruce, and lowland fir can endure

the shade of these forests, and that except in open places Douglas spruce, western larch, bull pine, and lodgepole pine are ruled out altogether. The birch is found scattered throughout the limits of the forest. Indeed, as will be shown, it is often a conspicuous tree



FIG. 23.—Mature lodgepole pine forest in Swan valley, showing a dense stand in which the trunks are 15 to 20cm in diameter; the undergrowth consists of *Acer glabrum*, *Pyrola*, *Pteridium*, *Linnaea*, etc.—Photograph by McCALLUM.

in the burns, and grows up with lodgepole pines, though as the forest matures it drops out early. The undergrowth consists of *Acer glabrum*, *Lepargyrea canadensis*, *Symphoricarpos* sp., *Rosa* sp., *Lycopodium* sp., *Pyrola secunda*, *Pteridium aquilinum*, *Linnaea borealis*, *Chimaphila umbellata*, *Clintonia borealis*, and *Aralia nudi-*

*caulis*. Scattered specimens of juniper are found in places. In other respects the forest is like the other stands in the mesophytic regions.

In what has been said concerning fires, no mention has been made of species other than conifers. They may often play an important rôle in the first stages in the natural process of reforestation, but their importance diminishes as the life history becomes complete. One of the first plants to give a decided aspect to the forest after fires is the fireweed (*Chamaenerion angustifolium*). The birch and aspen, by virtue of their light seeds, gain an early place in the burns. Indeed sometimes their stands become quite dense and they check the advent of coniferous species. Many species that were on the forest floor of the mature stand may have survived the fires and spring up even more vigorously than before, because the shade has been removed. Especially is this true of those forms that can send shoots from their roots or from underground stems. In the burn on the east slope of the Mission Range south of Big Fork, there are shrubby growths of *Salix* spp., *Ceanothus sanguineus*, *Opulaster pauciflorus*, *Acer glabrum*, and *Holodiscus ariaefolia*, many of which probably were present as underbrush in the stand that existed previous to the burn. These shrubs will retard the reforestation of the area in some instances to a marked degree. If the forest that is destroyed be on the border of the prairie, plants from that association will form an important element in the growth that follows. This is of course detrimental to forest growth. Indeed if the fires be repeated often enough, the forest plants will gradually diminish in quantity, and the prairie element will become more and more prominent, until finally a prairie will come to replace a forest. If the fires be checked, however, for any length of time, the forest will gradually reconquer the territory thus lost. It is probable that some of the prairie region in Flathead valley has been won from the forest in this manner. It must be remembered that in the area bordering on the prairie, in Flathead valley at least, lodgepole pine is not successful and is thus ruled out from playing any important rôle in these places after fires.

In the discussion of the causes for the Nigger Prairie region, mention was made of the importance of the accumulation of humus in rendering the sandy soil more capable of holding moisture. It

can be seen that fires will tend to reduce the humus content of the soil. This is of extreme importance, for that which would otherwise add to the richness of the soil and increase its water-holding capacity is destroyed. Especially is it of importance in those regions that border on the prairie. There is evidence of many such surface fires in the open woods around Nigger Prairie, and it is very probable that these fires have played an important rôle in keeping the prairie vegetation from being encroached upon by the forests that surround it. Even in the mesophytic conditions, fires influence the capacity of the soil to reforest itself quickly, by partially or totally destroying the humus. However, with the reclothing of the burned area, the floor of the new forest will gradually resume its normal condition.

From the above it will be seen that forest fires play an important part in determining the composition of the forest. That forest fires prevailed in this region before the advent of civilized man is a logical inference. In the lodgepole pine forest in the Swan River there are unmistakable signs of fires before the present forest, which is now about one hundred years old, was started. How these fires started can only be conjectured, and it is not within the province of this paper to discuss their origin. It is also very evident that the fires are more numerous since the settling of the country by civilized man than before.

#### SUMMARY.

1. Fires play an important part in determining the present composition of the forest.
2. The lodgepole pine is the "fire tree" of the region.
3. It is favored after fires principally because it has the capacity to produce seeds early in its life.
4. Many complex conditions of growth are introduced after fire. The species that have seed-bearing trees near the burn will generally be represented in the new forest.
5. Repeated burnings at intervals of ten to thirty years will establish a lodgepole pine forest where formerly there existed a normal mesophytic forest.
6. Repeated burnings at intervals of five years or less will destroy all forest growth.

7. After the lodgepole forest is once established and the fires are checked, it will slowly be replaced by the species that exist in the normal forests.

8. The lodgepole pine is not successful in the bull pine belt.

I wish to thank Dr. H. C. COWLES for many valuable suggestions made in the preparation of this paper; also Professor M. T. ELROD, through whose kindness I was permitted to make the Montana Biological Station headquarters while collecting data; also Professor ELROD, W. E. PRAEGER, and W. B. MCCALLUM for the photographs from which the illustrations were made. The taxonomic nomenclature used in this paper is that found in RYDBERG's *Catalogue of the flora of Montana and the Yellowstone National Park*, and SUDWORTH's *Check list of the forest trees of the United States*.

GOVERNMENT LABORATORIES,  
Manila, P. I.

## BRIEFER ARTICLES.

### NOTES ON THE PHYSIOLOGY OF STIGEOCLONIUM. CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. LXX.

(WITH THREE FIGURES)

THE experiments with which this paper has to deal fall into two groups, those with low temperatures and those with sea water. The subject for experimentation was the polymorphic form of *Stigeoclonium* with which I have been concerned in several preceding papers.<sup>1</sup> As has been already shown, this alga takes either of two very distinct forms according to the nature of the medium in which it is grown. In solutions of relatively high osmotic pressure and in those of low pressure to which stimulating metallic salts have been added, the palmella form is assumed. This consists of nearly spherical cells lying singly or in irregular groups. In unpoisoned solutions of low osmotic pressure the alga grows as branching filaments composed of cylindrical cells. When such filaments are placed in a poisoned solution or in one of high pressure, they become transformed to the other form by the simple rounding off of their individual cells. In general the production of zoospores is checked where the palmella form is produced, but there are a number of exceptions to this among the metallic poisons.<sup>2</sup> In such cases this process may be accelerated even where the germination and growth of the zoospores are inhibited.

I. *Low temperatures*.—Since high pressure of the medium acts to prevent water absorption, and since low temperatures are known to cause the extrusion of water by both plant and animal cells,<sup>3</sup> it occurred to me that

<sup>1</sup> LIVINGSTON, B. E., (1) On the nature of the stimulus which causes the change in form of polymorphic green algae. *BOT. GAZETTE* 30:289-317. 1900.

———, (2) Further notes on the physiology of polymorphism in green algae. *BOT. GAZETTE* 32:292-302. 1901.

———, (3) The rôle of diffusion and osmotic pressure in plants. Chicago. 1903. Part II, Chapter III. This chapter was reprinted as "The effect of the osmotic pressure of the medium upon the growth and reproduction of organisms. Chicago. 1903.

———, (4) Chemical stimulation of a green alga, *Bull. Torr. Bot. Club* 32:1-34. figs. 17. 1905.

<sup>2</sup> Loc. cit. (4).

<sup>3</sup> Loc. cit. (3), pp. 75 and 141, and the references there given.

possibly low temperatures might also cause filaments of this alga to take the palmella form. Experiments were devised to test this point, and their results are here given.

Cultures of the filamentous form were made in small glass dishes with loosely fitting covers. The medium employed was the modification of Knop's solution previously described,<sup>4</sup> and had an osmotic pressure of 60<sup>mm</sup> of mercury. The culture dishes were placed in weighted beakers which floated about three-fourths immersed in ice-water contained in a galvanized iron tank. Ice was added from time to time as melting took place, and the superfluous water was drawn off. The tank was covered with glass and stood in the conservatory, so that the plants were supplied with the necessary light for growth. The cultures were shaded from direct sunlight.

In the medium employed the alga grows rapidly as filaments at laboratory and conservatory temperatures. Zoospores are produced and germinate to form new filaments. Such normal filaments are shown in *fig. 2*. The figures are all from camera drawings and are magnified about 300 diameters. In the cold cultures, whose temperature rarely rose above 6° C.,<sup>5</sup> the growth of the original filaments was checked, but the production of zoospores continued at about the normal rate. At the end of fifteen days the old filaments had completely changed to the palmella form, in the manner already described for solutions of high osmotic pressure. Zoospores fail to germinate normally in the cold; most of them simply lie quiescent on the bottom of the dish, having assumed the spherical form, while a few enlarge slowly and divide into new palmella cells. Growth of the palmella form is comparatively very slow at ordinary temperatures. It is still more so in the cold, and this retardation is here even more marked in resting zoospores than in cells produced by the breaking up of the original filaments. Palmella cells from one of the cold cultures are shown in *fig. 1*. They are seen to be exactly similar to those produced by high pressure or toxic cations. Several resting zoospores and empty sporangia are also figured. That the plant was not permanently injured by the low temperature was shown conclusively by continuing the cultures in the conservatory after they had been taken from the cold bath. They all responded to the return to normal temperature, by producing typical filaments in from ten to fourteen days. A portion of one of these cultures after the filamentous form had been assumed again is shown in *fig. 2*. Germinating zoospores and empty sporangia are also shown.

<sup>4</sup> Loc. cit. (4), p. 4.

<sup>5</sup> During the period of the experiment, 20 days, the temperature was unwittingly allowed to approach 10° C. several times, for periods of a few hours only.



Five cultures made from different stock material, and always compared with controls maintained at the temperature of the conservatory, all agreed perfectly in the results. Thus it seems safe to conclude that *low temperatures act upon the vegetative growth of this alga with the same result as do high osmotic pressure and poison cations*. No acceleration of zoospore formation, a phenomenon often exhibited in poisoned solutions, has been observed here. It appears that in low temperature we have another method of withholding water from the plant, and that the uniform response to such withholding is the production of the palmella form.<sup>6</sup>

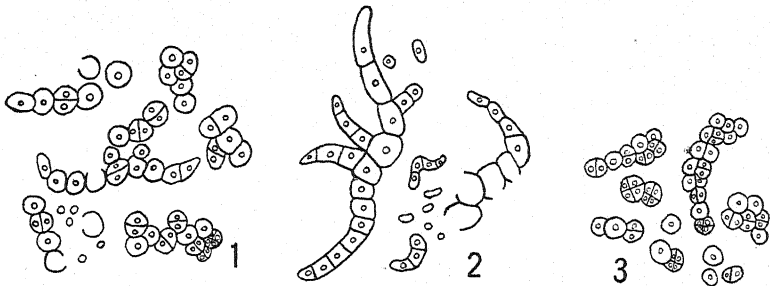


FIG. 1.—Palmella from filaments like fig. 2 in culture at low temperature.

FIG. 2.—Normal filaments and germinating zoospores from cold palmella culture returned to normal temperature.

FIG. 3.—Palmella in sea water from normal filaments like fig. 2.

II. *Sea water*.—During my residence at the New York Botanical Garden I was able to determine the behavior of this *Stigeoclonium* in sea water. Natural water was collected from the surf at Far Rockaway, L. I., and was brought in bottles to the laboratory, where it was used in making the cultures. Filaments of this plant placed in undiluted sea water take the typical palmella form, as in other solutions of high pressure. Zoospores are not produced, nor do those produced previously germinate. Such a culture is shown in fig. 3. The water used had a pressure of about 25,000<sup>mm</sup> of mercury.<sup>7</sup> In sea water diluted to one-tenth and one-hundredth of its natural concentration respectively—water redistilled in glass being used in the dilution—the response is the same, although the change is not so rapid. In the latter dilution it seems impossible that osmotic pressure is the main stimulating factor, for here is a pressure of only about 250<sup>mm</sup>

<sup>6</sup> See the remarks on this subject in the paper on chemical stimulation, loc. cit. (4), p. 21 et seq.

<sup>7</sup> The calculation was made by the method of the depression of the freezing-point, loc. cit. (3), p. 37.

of mercury, while a pressure of over 15,000<sup>mm</sup> is necessary to bring about a marked response in the alga.<sup>8</sup> Perhaps there is a stimulating chemical in sea water which aids the somewhat high osmotic pressure to bring about the result. At a dilution of one-thousandth the filaments grow normally as in weak nutrient solutions.

The result of this test suggests how a fresh-water form coming into sea water may be influenced to change its character and still live and thrive. This may have been a factor in the evolution of certain algal forms.—BURTON EDWARD LIVINGSTON, *The University of Chicago*.

#### FERTILIZATION IN THE SAPROLEGNIALES.

PROFESSOR B. M. DAVIS,<sup>9</sup> in his criticism of my views "On fertilization in the Saprolegnieae," makes use of the term "ovocentrum" in a sense very different from that which I gave to it. His use of the term, moreover, is obviously based on a misconception of my meaning. He says "TROW calls the egg-asters ovocentra." I neither do this, nor do I approve of it being done. Such an innovation would be worse than useless, as it would increase the confusion which already exists. At present, unfortunately, structures of more than one kind have apparently been grouped together by giving them a common name—"coenocentrum." I suggested the term "ovocentrum" as suitable for use in describing the dense mass of protoplasm found at the center of the eggs of the Saprolegnieae. Imbedded in the ovocentrum of an egg I find a single nucleus accompanied by a single centrosome and its astrosphere. It would have been correct, I think, for DAVIS to have said that the "coenocentra" discovered by him in Saprolegnia were interpreted by me—rightly or wrongly—as consisting of centrosomes with their astrospheres. The "ovocentra" of the Saprolegnieae may be the equivalents of the coenocentra of the Peronosporae. They are altogether different from centrosomes and astrospheres. I cannot, therefore, accept DAVIS's statement that I call "the egg-asters ovocentra." I do not propose to discuss the many other points of interest raised by Professor DAVIS, for new facts are required now, and these can only be obtained by patient and prolonged investigation in the laboratory.—A. H. TROW, *Cardiff, Wales*.

<sup>8</sup> Loc. cit. (1) and (2).    <sup>9</sup> BOT. GAZETTE 39:61. 1905.

## CURRENT LITERATURE.

### BOOK REVIEWS.

#### The trees of North America

PROFESSOR SARGENT<sup>1</sup> has brought into a convenient volume the information concerning the trees of North America that is much more elaborated in his *Silva*. The sequence is that of ENGLER and PRANTL'S *Die natürlichen Pflanzenfamilien*. Especial attention has been given to the construction of simple analytical keys, so that a species may be determined with the minimum of trouble. For example, the key to the families is based on the arrangement and character of the leaves; and in the same way genera and species are reached by the important and easily discovered contrasting characters. Each of the 630 or more species is further made clear by the admirable illustrations of Mr. C. E. FAXON, showing the leaves, flowers, and fruits. There is no reason why this manual should not become at once extensively used by all those interested in trees, a constituency that extends far beyond the boundary of professional botanists.—J. M. C.

#### Organic evolution

A RECENT BOOK by Professor METCALF<sup>2</sup> presents in a clear and simple style the fundamental principles of organic evolution in a form very well adapted to the needs of the general reader and to those who wish an outline of the theory of Darwinism. The standpoint is clearly that of the Neo-Darwinist, and the main topics the familiar ones of adherents of this school. Perhaps the most striking feature of the book is the wealth of clear and very well selected illustrations, a large proportion of which are presented for the first time in a general text of this character. These give to the work a character quite its own, and in themselves justify a book which in its general outlines follows very closely the subject-matter and method of presentation in several popular accounts of evolution, including those of WALLACE and ROMANES. The subject-matter is chiefly zoological, and the book would hardly claim an extensive treatment of the principles of plant evolution.—B. M. DAVIS.

### MINOR NOTICES.

THE REPORT for 1904 of the Chief of the Bureau of Plant Industry, Dr. GALLOWAY, is commended to the perusal of all botanists that they keep in touch with the botanical work in progress under this Bureau of the Department of

<sup>1</sup> SARGENT, CHARLES SPRAGUE, *Manual of the trees of North America* (exclusive of Mexico). Imp. 8vo. pp. xxiii+826. figs. 640. Boston: Houghton, Mifflin and Company. 1905. \$6.00.

<sup>2</sup> METCALF, M. M., *An outline of the theory of organic evolution*. Imp. 8vo. pp. 204. pls. 101. figs. 46. New York: The Macmillan Co. 1904.

Agriculture. It is impossible here to summarize the report, itself a summary. Certainly every American who understands the past success and future plans of this bureau must feel proud that our government is thus leading the world in turning applied botany, based upon researches by a capable staff, to the production of wealth and comfort for the people. As a mere matter of dollars and cents, any one of a dozen or more discoveries made or practically applied by this bureau recently will add to the annual income from our fields and gardens more than the whole bureau has cost from its beginning. The report is a concise and clear showing that will interest all and will surprise those who have not followed closely the recent developments.—C. R. B.

THE BULLETIN from the laboratories of natural history of the State University of Iowa contains in its last issue (Vol. V, no. 4) two botanical papers on the local flora, viz., *The flora of the St. Peter sandstone in Winnesheik Co., Iowa*, by Professor B. SHIMEK: and *The Discomycetes of eastern Iowa*, by FRED J. SEAVER. In the latter, out of nearly one hundred species collected in the state, about fifty are described and illustrated in twenty-five plates, the remainder being reserved for further study. No new species are described.—C. R. B.

THE SECOND ANNUAL ISSUE of the volume on Botany of the *International Catalogue of Scientific Literature*<sup>3</sup> was published in December last, the manuscript having been completed in March 1904. There is no occasion to explain the scope and quality of this publication, for it has already been extensively reviewed,<sup>4</sup> and the opinions of botanists concerning it have become well settled.—J. M. C.

J. PERKINS<sup>5</sup> has issued the third fascicle of contributions to the flora of the Philippines. The collaborators are as follows: C. DE CANDOLLE, Piperaceae; J. PERKINS, Rutaceae; O. WARBURG, Ulmaceae, Moraceae, Urticaceae, Balanophoraceae, Aristolochiaceae, Magnoliaceae, Thymelaeaceae, Ericaceae, and Ficus; E. B. COPELAND, Ferns (38 n. spp. and *Christopteris*, n. gen.).—J. M. C.

#### NOTES FOR STUDENTS.

RECENT STUDIES IN HYBRIDIZATION.—The literature of Mendelian inheritance has been enriched by the appearance of several important recent papers. TSCHERMAK<sup>6</sup> gives an account of further studies in the hybridization of peas, stocks (*Matthiola*), beans, etc., which have given him so many noteworthy results reported in earlier contributions. The great amount of interesting detail makes adequate review impossible in a short note. "Kreuzungsnova," which have

<sup>3</sup> International Catalogue of Scientific Literature. M. Botany. 2d annual issue. 8vo. pp. 1111. London: Harrison & Sons, 45 St. Martin's Lane. 1904. 37s. 6d.

<sup>4</sup> BOT. GAZETTE 34:455. 1902.

<sup>5</sup> PERKINS, J., *Fragmenta Florae Philippinae*. Fasc. III. pp. 153-212. *pl.* 4. Leipzig: Gebrüder Borntraeger. 1905. M5.

<sup>6</sup> TSCHERMAK, E., *Weitere Kreuzungsstudien an Erbsen, Leukojeu und Bohnen*. Zeits. Landw. Versuchsw. 7:533-638. 1904.

usually been considered uncommon, he has found to result regularly in seventeen of the hybrids that he reports. Races which show the possession of such latent characters that are externalized as a result of crossing he has designated in another recent paper<sup>7</sup> as "cryptomeric" races, and the process of externalization of latent characters as "crypto-hybridism." In many cases the new characters are recognizable as atavistic, in other cases they appear to be retrogressive or degressive modifications. The processes by which these arise he calls "hybrid atavism" and "hybrid mutation," and he looks upon the latter as an important source of new forms, especially of "defect-races."

In nearly all cases the new characters as well as the parental characters behaved in a Mendelian way. Thus in a cross between two races of peas, white-flowered  $\times$  rose-colored gave complete dominance of red (atavistic) in the first generation ( $F_1$ ) splitting in  $F_2$  to red: rose: white = 9:3:4, the red dominating the rose, and red + rose the white, in the simple ratio 3:1. In a case of this kind the red is called "dominant" and rose "co-dominant." In other cases "co-recessives" occurred, giving four forms in the second generation, the ratio being 9:3:3:1. A still further complication was found in a cross between white-flowered *Matthiola glabra* and red-flowered *M. incana*, in which pure violet dominated in  $F_1$  and five forms appeared in  $F_2$ , giving approximately the proportions 27:9:9:3:16. This last result was reported by TSCHERMAK two years ago, and he explained it by assuming that each of the four colors (the fifth class being the white recessives) is a compound,  $a+b$ ,  $a+d$ ,  $b+c$ , and  $c+d$ , and on this assumption he predicted then what would be the product of each of these groups in  $F_3$  when self-fertilized. The third generation is here presented, showing that in every instance his prediction was confirmed.

LOCK<sup>8</sup> obtained very similar results in crosses of various cultivated peas with species native at Peradeniya, Ceylon. Thus with respect to seed-color, self-colored  $\times$  white gave in  $F_2$  self-colored: purple spotted: white = 9:3:4, and another case precisely resembling that of TSCHERMAK's *Matthiolas* gave categories of seed-coloration in the second generation nearly in the ratios 27:9:9:3:16. The explanation offered by LOCK is essentially the same as TSCHERMAK's, though differently expressed. He assumes that the allelomorphs ABC in the colored pea are matched by corresponding recessives abc in the white, but that neither B nor C can reach external expression except in the presence of A. The chance combinations of gametes containing these allelomorphs then result in the observed ratios.

LOCK's paper gives an admirable general treatment of Mendelism, illustrated with new examples taken from his own studies, and presents briefly but fairly the results of other workers. It can be recommended to any one who wishes to

<sup>7</sup> TSCHERMAK, E., Die Theorie der Kryptomerie und des Kryptohybridismus. Beihefte Bot. Centralbl. 16:11-35. 1904.

<sup>8</sup> LOCK, R. H., Studies in plant breeding in the tropics. Ann. Roy. Bot. Gard. Peradeniya 2:299-356. 1904.

orient himself with the least possible expenditure of time and effort in the important fields which have been opened up by MENDEL and his belated successors.

EMERSON<sup>9</sup> gives a continuation of his studies in bean hybrids, in which he now treats his results statistically, instead of qualitatively as in his preliminary report two years ago. The numbers are mostly not large, but considering the smallness their agreement with the theoretical ratios is fairly close. The chief interest in EMERSON'S results is the class of characters investigated, often making classification difficult, and considerable error probably being introduced in this way. A few of these characters with the dominant member of the pair given first are as follows: running habit (flowers axillary), bush habit (flowers terminal); pods tender, pods tough; pods green, pods yellow. In the case of stringless *vs.* stringy pods, about half the crosses showed the former dominant, the other half being intermediate; though all the progeny from any given cross behaved consistently. EMERSON shows that no prediction can be made regarding the hereditary behavior of seed-color from knowing the relations obtaining in other hybrids having the same seed-color, a fact also noted by TSCHERMAK in the first paper mentioned above.

CORRENS<sup>10</sup> has reported the results of further observations on hybrids of *Hyoscyamus niger*, *H. pallidus*, and *H. major*. The former crossed with its var. *annuus* shows complete dominance of the biennial habit with typical splitting in  $F_2$  and later generations. *H. pallidus*  $\times$  *H. niger*, which was reported in a previous paper as giving intermediate flower color in  $F_1$ , is now shown to split typically in later generations, regardless of the annual or biennial habit of the offspring and independently of environmental conditions.

CORRENS<sup>11</sup> has also investigated the hereditary relations of gynodioecism, dealing chiefly with *Satureja hortensis* and *Silene inflata*. In the former species bisporangiate flowers crossed together showed a predominance of bisporangiate plants in  $F_1$ , but when stigmas of the ovulate plants were pollinated with pollen from bisporangiate plants the offspring were almost without exception ovulate. In *Silene* the results were very similar,  $\sigma \times \sigma$  giving almost entirely  $\sigma$ , and  $\sigma \times \varphi$  resulting in a predominance of  $\varphi$ . This is quite contrary to Mendelian expectation, and the author does not believe that sexuality can be aligned under ordinary laws governing characters of hybrids, which it will be recalled has been attempted by CASTLE<sup>12</sup> with reference to animals.—G. H. SHULL.

<sup>9</sup> EMERSON, R. A., Heredity in bean hybrids. Ann. Rept. Agr. Exp. Sta. Nebraska 17:33-68. 1904.

<sup>10</sup> CORRENS, C., Ein typisch spaltender Bastard zwischen einer einjährigen Sippe des *Hyoscyamus niger*. Ber. Deutsch. Bot. Gesells. 22:517-524. 1904.

<sup>11</sup> CORRENS, C., Experimentelle Untersuchungen über die Gynodioecie. Ber. Deutsch. Bot. Gesells. 22:506-517. 1904.

<sup>12</sup> CASTLE, W. E., The heredity of sex. Bull. Mus. Comp. Zool. 40:187-218. 1903.

PENHALLOW<sup>13</sup> has recently published the first and general part of an extensive treatise on the anatomical determination of the North American Coniferales as well as certain species from Japan and Australia. The memoir represents the results of a quarter of a century's work in this field and is of great importance from the paleobotanical and phylogenetic standpoints. Although the author expresses his appreciation of the value of a general anatomical study of the group, he limits himself to the structural features of the ligneous cylinder, for the reason that coniferous remains are ordinarily best preserved as fragments of wood. Wood structure is discussed under the following headings: spiral tracheids; bordered pits, distribution and structure; medullary rays; resinous tracheids and resin cells; and resin passages.

Under the caption of bordered pits, the author points out that multiseriate and crowded pits deformed by mutual pressure are characteristic of the older gymnosperms, the Cycadofilices, Cordaitales, etc. Bordered pits are in general confined to the radial walls of the tracheids, exceptions to this mode of distribution occurring only in the primary wood and in the autumnal tracheids of the annual rings. Under the heading of medullary rays, the various types of structure which are of diagnostic importance are clearly and definitely described, and in this respect the present work marks a long advance on its predecessors. Two types of ray are distinguished, namely the linear ray made up of a single series of cells, and the more complex fusiform ray, which is so broad as to contain a horizontal resin canal. Resinous tracheids are described as diagnostic for the Araucarineae, but also occur sporadically in certain species of *Abies*. Resin cells, according to the author, appear in the more primitive conifers (exclusive of the yew-like *Taxineae*) and are characterized by their scattering, zoned, or segregated distribution, the latter condition being considered the most specialized. Where the resin-cells are highly segregated they may give rise schizogenously to resin cysts of limited extent, with walls constricted at intervals. Resinous cysts are found characteristically in the abietineous genera *Tsuga* and *Abies*, but also occur in living and extinct *Sequoias*. In the abietineous genera *Larix*, *Pseudotsuga*, and *Picea*, the resin spaces form a continuous system of vertical and horizontal passages, which according to the author betray their derivation from resin cysts by the constricted character of their walls. In *Pinus* the resin passages no longer show signs of constriction and are moreover lined entirely with thin-walled epithelium.

The author, as the result of plotting frequency curves based on the occurrence of the various characters of the wood, reaches certain conclusions as to phylogeny which may be briefly stated as follows: The *Taxaceae* are the oldest of the Coniferales, and from their general plexus have branched off on the one hand the *Podocarpeae*, and on the other the common trunk, which gave rise to the *Taxo-*

<sup>13</sup> PENHALLOW, D. P., The anatomy of the North American Coniferales together with certain exotic species from Japan and Australia. Part I. *American Nat.* 38: 243-273, 331-359, 523-554, 691-723. 1904.

dineae, Cupressineae, and Abietineae in approximately ascending order. The Araucarineae, contrary to the usual opinion, have a separate and direct origin from the Cordaitales. The conclusions reached by the author from the study of wood harmonize on the whole very well with those adopted in general taxonomic works such as Engler and Prantl's *Die natürliche Pflanzenfamilien*, and are based on the assumption that greater complexity of structure is necessarily characteristic of more modern forms. There is of course room for difference of opinion on this subject, in view of the evidence of general paleobotany, comparative anatomy, and development, which seems to show that the Coniferales form a series of recession rather than of progression. There can be no doubt, however, as to the very important character of the facts brought out by the investigations of Professor PENHALLOW, and the second part of the memoir, which is to contain the specific determinations of the conifers from the structure of their wood, will be awaited with interest.—E. C. JEFFREY.

JEFFREY<sup>14</sup> has published the second of his contributions to our knowledge of the anatomy of the Coniferales, in so far as it bears upon relationships and phylogeny. The immense service that anatomy of this kind is rendering to morphology that concerns itself with phylogeny cannot be overestimated. The student of gymnosperms is particularly indebted to JEFFREY for the studies he is just now prosecuting, for this new method of attack could not have been directed more usefully than upon Coniferales. In the preceding number of the series the author has reached the conclusion that *Sequoia* shows an abietineous origin, and it was natural that a presentation of the Abietineae should follow. No better summary of his results could be given than that prepared by the author himself; and since the subject is one of much general interest and importance no apology is needed for reproducing it here.

1. The Abietineae are divisible, on the evidence supplied by a study of their vegetative and reproductive organs, into two distinct subfamilies, viz., the Pineae and the Abietae.

2. The Pineae are characterized by the invariable presence of resin canals, forming an anastomosing system in the secondary wood and cortex of root and shoot. Resin canals are present in the outer margin of the primary wood of the root. The scales of the female cone are not deciduous. *Pinus*, *Picea*, *Larix*, *Pseudotsuga*.

3. The Abietae ordinarily do not possess resin canals in the secondary wood of root and shoot. Resin canals, however, are sometimes found in the wood of the female reproductive axis, and in the first annual ring of vigorous shoots of sexually mature trees. Resin canals occur in the secondary wood in tangential rows, as a result of injury. Resin canals are invariably found in the center of the primary wood of the root. The scales of the female cone are generally deciduous. *Abies*, *Pseudolarix*, *Cedrus*, *Tsuga*.

4. The evidence derived from anatomy and experimental morphology goes to show that the presence of resin ducts in the woody tissues and in the cortex of the Abietineae

<sup>14</sup> JEFFREY, EDWARD C., The comparative anatomy of the Coniferales. Part 2.—The Abietineae. *Memoirs Boston Soc. Nat. Hist.* 6:1-37. pls. 1-7. 1904.



is primitive for the group. The resin canals persist longest in the reproductive axis, the leaf, and the *first* annual ring of root and shoot. In the more specialized genera the resin canals of the wood are replaced by resin cells, but in the latter condition of the wood, resin canals may always be recalled as a result of injury. The disappearance of resin canals and their replacement by resin cells is probably for the sake of economy of carbohydrate material. In *Pseudolarix* and *Tsuga* even the cortical resin canals disappear from all organs except the female reproductive axis, together with its appendages, and the vegetative leaf.

5. The Abietineae are an older group than the Cupressineae, in the larger sense, and are either antecedent to these or from the same ancestry. This conclusion is reached from an anatomical and experimental morphological study of their organs, root, shoot, and leaf. It is confirmed by the examination of the female reproductive organs and of the pollen. It is further in conformity with paleontological evidence.

6. The Abietineae are throughout characterized by the same double leaf trace which is a constant feature of the older gymnosperms, the Lyginodendreae, the Cordaitales, the Ginkgoales, and the Cycadales. This feature serves to separate them from the Cupressineae in the larger sense, and to unite them with the Cordaitales, which they resemble in other important particulars, described in the body of the memoir.

7. The Abietineae must be regarded on comparative anatomical and morphological grounds as a very ancient order of the Coniferales, and may even be the oldest living representatives of this group.—J. M. C.

SKOTTSBERG,<sup>15</sup> botanist of the Swedish Antarctic Expedition of 1901-1903, gives a preliminary report on the phytogeographical conditions in the Antarctic regions. He proposes for the lands south of 40-50° S. the following names: *Austral* zone, including Terra del Fuego, with the Isla de los Estados, the Falkland islands, South Georgia, and no doubt the South Sandwich islands; and *Antarctic* zone, including South Orkney and South Shetland islands, and Graham Land. An objection must be raised against the use of the terms Antarctic and Austral for local geographical areas such as the author is speaking of. The reviewer had recently (in a paper read before the Philadelphia meeting of A. A. A. S. 1904) occasion to mention in passing that the name of Austral zone for a certain phytogeographical area of North America was incorrect, and he holds a similar opinion in regard to SKOTTSBERG's use of the term. What is to be called the Austral zone? Certainly not a limited area in South America with a few neighboring oceanic islands. We have at present an almost endless number of phytogeographical divisions, and this is not the place to enter upon a discussion of the relative merits of these, but it seems proper here to point out that if we are ever to get a consistent nomenclature in phytogeography it will not do to apply to local or minor areas names generally used to designate larger divisions. The Arctic region is recognized by DRUDE and ENGLER, for example, as a subdivision of what the former calls the Northern realm and the latter the North extratropical realm. MERRIAM gives to this Northern realm the name Boreal region. The reviewer

<sup>15</sup> SKOTTSBERG, C., On the zonal distribution of South Atlantic and Antarctic vegetation. *Geographical Journal* 655-664. 1904.

would call it the Boreal realm, of which the Arctic region constitutes a part. In the southern hemisphere we have a corresponding Austral realm, of which the Antarctic region is a subdivision. What SKOTTSBERG now calls the Austral zone is a region that may be designated as Patagonian, or Fuegian, or Magellanian, or by some other local name, and which is a division of equal rank to the Antarctic, subordinating this and several other regions under the term Austral realm. Our criticism here refers to the use of the terms only, not to the author's definition or limitations of the areas under consideration. In regard to the flora of the South Atlantic ocean, the author considers that the division into Austral and Antarctic is just as evident as in the land flora. Until the detailed results of the expedition are made known and until this question is thoroughly discussed, final judgment in the case must be reserved.—OLSSON-SEFFER.

IN A PAPER READ before the B. A. A. S. last August, CZAPEK presents<sup>16</sup> a fuller account of his researches on the anti-ferment reaction which occurs in tropistic movements, especially of roots. In geotropically stimulated roots, for instance, homogentisinic acid, a product of decomposition of tyrosin by tyrosinase, accumulates slightly, instead of being oxidized at once, because an anti-enzyme is produced by the stimulation, which inhibits the action of the oxidase. The quantitative determination of the homogentisinic acid is not practicable as a measure of the reaction, but a solution of homogentisinic acid may be used as a reagent for determining by titration the retardation of its oxidation by the anti-oxidase. The roots to be tested are ground in water with powdered glass to a thin paste, and a standard solution of homogentisinic acid added; the initial reducing power of the wash is determined, and repeatedly at intervals of five days, by titration with  $n/10$   $\text{AgNO}_3$ . CZAPEK finds that only tropisms produce the anti-enzyme; narcosis, poisoning, mechanical hindrance of growth, and wounding having failed by themselves to produce the reaction. Six minutes was determined to be the limit for roots placed horizontal at  $17^\circ$  C. to show the anti-enzyme reaction, which persists for about four hours. Though not observably intensified by prolonged stimulation of the root, it persists for a much longer time, even up to thirty hours after fifty minutes stimulation. The reaction becomes certain for thirty minutes induction at an angle of  $7^\circ$  from the normal and at  $10^\circ$  is maximal, remaining constant up to  $170^\circ$ ; decreasing very much at  $176^\circ$ , and not showing at all at  $180^\circ$ . By reducing the time of induction it can be shown that the reaction is stronger at  $135^\circ$ – $150^\circ$  than at horizontal, which assists in settling a disputed point. Roots rotated on the klinostat show the reaction, clearly supporting the view that geotropic stimulation occurs under such conditions though curvature does not result. This reaction also confirms CZAPEK'S experiments with glass slippers, showing that more than the root cap with its statolith cells is involved in the geotropic phenomena. He lists these phenomena (assuming them to be consecutive) thus:

<sup>16</sup> CZAPEK, F., The anti-ferment reaction in the tropistic movements of plants  
Ann. Botany 19:75-98. 1905.

(1) statolith effect; (2) anti-ferment reaction; (3) the processes hindered by shock; (4) transmission of stimulus; (5) curvature.—C. R. B.

A NOTABLE FEATURE of the recent meetings of the affiliated scientific organizations at Philadelphia was the annual discussion before the American Society of Naturalists, which this year had for its subject the mutation theory. Two of the seven addresses were botanical, D. T. MACDOUGAL opening the discussion from the standpoint of plant-breeding, and L. H. BAILEY presenting the taxonomic bearing of the theory. In the opening address MACDOUGAL<sup>17</sup> stated the main thesis of the mutation theory thus: "the saltatory movement of characters, regardless of the taxonomic value of the resultant forms," its principal corollary being "that the saltations in question do result in the constitution of new species and varieties." He believes that many current misconceptions regarding species are due to the failure to discriminate between elementary species and the composite or "group" species of the systematist; and that there is accumulating evidence that the supposed deleterious effects of close-fertilization are groundless. Warning is given of the confusion which must arise through the unguarded use of the terms "mutation" and "variation" to designate phenomena of segregation and alternative inheritance in hybrid strains. It will be recalled in this connection that in a previous paper MACDOUGAL<sup>18</sup> has discussed the difference between fluctuating and mutative variations, and has included as mutative variations only "newly arisen and transmissible qualities," emphasizing the fact that it is a pure presumption to designate any aberrant condition a mutation until its hereditary character has been demonstrated. Regarding the causes of mutations little is known, but the results of the mutation cultures both at Amsterdam and at New York are held to indicate that they arise in greater numbers under environmental conditions which are especially favorable for vegetative development and seed-production. Some mutations occur much more frequently than others, and the highest total number of mutants found in any progeny of *Onagra Lamarckiana* in New York was over six per cent., as compared with the five per cent. maximum observed by DE VRIES in Amsterdam. Report on other mutating species is promised for the near future.—G. H. SHULL.

THE ECONOMIC importance of LUTHER BURBANK's achievements in plant breeding, and a certain mystery which has surrounded his work owing to his inability or unwillingness heretofore to impart information regarding the methods he uses, have won for him the appellation "wizard of horticulture." An attempt<sup>19</sup> to present to the public an account of the methods employed and some of the results obtained is welcome, and the name of President JORDAN adds to the

<sup>17</sup> MACDOUGAL, D. T., Discontinuous variation and the origin of species. *Torrey* 5:1-6. 1905.

<sup>18</sup> MACDOUGAL, D. T., Mutation in plants. *Amer. Nat.* 37:737-770. 1903.

<sup>19</sup> JORDAN, D. S., Some experiments of Luther Burbank. *Pop. Sci. Monthly* 66:201-225, figs. 22. 1905.

authoritative character of the account. The presentation is given in the form of quoted paragraphs from conversations with BURBANK, and the assurance is given that these have been referred to him for verification. This method certainly has advantages which to some degree counterbalance the disconnectedness and the frequent repetition of ideas which necessarily result from it. There is nothing new or unusual in the methods employed by BURBANK, namely, "selection, crossing, hybridization, and mutation," and it is apparent that his success is dependent upon his great activity rather than upon the methods used. This paper is of great scientific interest, but of little scientific value, and emphasizes with unusual force the difference between the economic and scientific ideals. It will be a source of information to scientists, but certainly of a great deal of misinformation to the general public, with whom the source of the statements made will carry a weight wholly incommensurate with their scientific value. It appears to the reviewer that the compiler of these paragraphs from BURBANK'S conversations owed it to his readers to explain two features of the technique employed which would lead to a correct valuation of the statements made. "Strawberry-raspberry hybrids" cause less surprise when it is known that insufficient precautions were taken to prevent the entrance of foreign pollen of unknown origin; similarly, when apple-trees grow from blackberry seeds it is well to bear in mind that the seeds were sown in unsterilized soil. The discussions of the mutation theory and other subjects bearing upon evolution will prove amusing.—G. H. SHULL.

ITEMS OF TAXONOMIC INTEREST are as follows: EDITH M. FARR (Contrib. Bot. Lab. Univ. Penn. 2:417-425. 1904) has described a new species of *Pachystima* from the Selkirk of British Columbia.—W. A. MURRILL (Bull. Torr. Bot. Club 31:593-610. 1904), in his ninth paper on the Polyporaceae, has described *Laetiporus*, *Trichaptum*, and *Pogonomyces* as new genera.—J. A. SHAFER (Torreya 4:177-181. 1904) has separated a new species of *Cassia* (*C. Medsgeri*) from *C. marilandica*.—In continuing their account of the flora of western Australia, L. DIELS and E. PRITZEL (Bot. Jahrb. 35:161-528. 1904) describe numerous new species and also a new genus (*Psammomoya*) of Celastraceae.—EDWARD L. GREENE (Leaflets 1:81-96. 1904) has segregated from *Streptanthus* many of the Californian plants that have been referred to it, and has established the following genera to include them: *Euchisia* (14 spp., 3 new), *Pleiocardia* (9 spp., 2 new), *Mitophyllum*, *Microsemia*, and *Mesoreanthus* (3 spp., 2 new); has replaced *Chlorogalum* Kunth by the older *Laoihoe* Raf.; has recognized *Aloitis* Raf. as represented by *Gentiana quinqueflora occidentalis* and adds two new species; and has described new species of *Batrachium* (2) and *Sophia* (2).—B. F. BUSH (Trans. Acad. Sci. St. Louis 14:181-193. 1904) has monographed the Texan species of *Tradescantia*, recognizing 18 species, 10 of which are new.—P. A. RYDBERG (Bull. Torr. Bot. Club 31:631-655. 1904), in his 13th "Studies on the Rocky Mountain flora," has described new species in *Dodecatheon*, *Gentianella*, *Gilia* (6), *Polemonium* (2), *Lappula* (2), *Oreocarya* (2), *Mertensia* (6), *Stachys*, *Mon-*

ardella, *Solanum*, *Pentstemon* (3), *Castilleja* (3), *Valeriana* (2), *Coleosanthus*, *Grindelia* (2), *Gutierrezia* (2), *Chrysopsis* (4), *Solidago* (6), *Oligoneuron*, *Chrysothamnus* (2), and *Aster* (5).—J. M. C.

LYON<sup>20</sup> has stated more in detail his views as to the phylogeny of the cotyledons of angiosperms. The monophyletic origin of angiosperms is argued with considerable fullness; a view which recent anatomical studies have helped to establish, and to which there is probably little dissent at present. The cotyledons are regarded as primarily haustorial organs, related phylogenetically to the so-called foot of bryophytes and pteridophytes; a view which seems to be well taken and cogently argued. The monocotyledonous condition is claimed to be the primitive one among angiosperms, the dicotyledonous condition being derived from it through the "bifurcation" of the originally single cotyledon. This last view is probably the only one that will meet serious opposition, since the recent studies of the comparative anatomy of the vascular systems of the two groups have contributed great strength to the view that monocotyledons have been derived from dicotyledons. However, this detail does not affect the general claim as to the nature of cotyledons. Beginning with the sporophyte of bryophytes, in which the body is differentiated into two regions called "sporophore" and "haustrium," the latter is traced through into the angiosperms and shown to include cotyledon, hypocotyl, and primary root. In fact, the hypocotyl is regarded as a new "haustrial" structure that is differentiated between the root and the sporophore. The term "protocorm" is used instead of "proembryo" for the undifferentiated embryo, and "metacorm" for the "plant body after the differentiation of its permanent members." The author announces that a paper is in preparation in which he "will endeavor to demonstrate the validity of his hypothesis concerning the phylogeny of the cotyledon."—J. M. C.

NĚMEC has brought additional facts to the support of the statolith theory of geotropic perception.<sup>21</sup> Roots from whose tips 1<sup>mm</sup> has been cut show geotropic curvatures after 20 hours, because the regenerating tip consists of cells with large mobile starch grains. Roots with 1.5<sup>mm</sup> removed remain straight, having no such new cells. The regeneration of the perceptive complex is not always complete before the root becomes geotropic, certain older cells often acquiring motile starch grains and perceptive sensitiveness. He also adduces further evidence from the behavior of inverted root-tips and replies to objections based upon the results with glass-capped roots, where thigmotropic curvatures (this in the face of NEWCOMBE's results) may enter. Against CZAPEK's objection, that the chemical differences between stimulated and unstimulated roots are observed whether the statocysts are present or not, it is suggested that there

<sup>20</sup> LYON, HAROLD L., The embryo of the angiosperms. *Amer. Naturalist* 39: 13-35. 1905.

<sup>21</sup> NĚMEC, B., Einiges über den Geotropismus der Wurzeln. *Beihefte Bot. Centrbl.* 17:45-60. 1904.

may be two kinds of perception, of which that by heavy starch grains alone leads to curvature, the other (e. g., by radial pressure) leads to the chemical changes—a strained answer. After defending his ideas against some criticisms by NOLL and by MIEHE, he pays his compliments to WIESNER's objections based on *Clivia nobilis* and *C. miniata*, the former being geotropic, while the latter is not. But NĚMEC finds both confirm the statolith theory, inasmuch as in *C. nobilis* there is abundant motile starch in the perigonal leaves, and none in *C. miniata*. Statolith starch is found widely distributed in mosses. It is wanting in certain geotropic liverworts (*Metzgeria furcata*), abundant in the strongly geotropic *Trichocolea tomentella*, and scarce in the weakly geotropic *Plagiochila asplenoides*.—C. R. B.

STRASBURGER<sup>22</sup> gives a popular but strictly scientific discussion of the genus *Alchemilla* as it occurs on the Grand Salève at Geneva. At least thirty-one species of this genus are found on this one mountain where LINNÉ recognized only three. No wide gaps separate these species, but their distinctive characters are fully constant in inheritance. The author contrasts the Linnean conception of species as an abstraction with the present conception in which a species is a real entity which he defines as a group of individuals that agree among themselves, and are separated from other species by definite characters that they inherit, however slight these characters may be. The species of *Alchemilla* are believed to be the result of a rather recent period of mutation, the evidence of its recency being found: (a) in the want of marked gaps between the species, which would result through the extinction of some species by natural selection; (b) the almost perfect development of stamens rendered functionless by the apogamous habit of nearly all species; (c) the marked development of nectaries that are likewise functionless and secrete no nectar. The species are regarded as apogamous rather than parthenogenetic since no reduction of the chromosomes occurs. No case of parthenogenesis in this sense is yet known among higher plants. *Alchemilla* is paralleled with two other noteworthy apogamous genera, *Taraxacum* and *Hieracium*, both of which likewise show numerous elementary forms, and it is suggested that the apogamous habit of these genera may have resulted through excessive mutation that introduced continuous hybridizations with attendant deterioration of the sexual processes.—G. H. SHULL.

IN AN ADDRESS before section K of the British Association, WARD<sup>23</sup> has given an extremely interesting review of the growth of our knowledge of parasitism among the fungi and bacteria, from the researches of DEBARY to the present time. The first part of the paper deals with the more important earlier discoveries which have marked distinct phases or epochs in the advancement of this subject, notably those of A. BRAUN, DEBARY, TULASNE, COHN, KOCH, and others.

<sup>22</sup> STRASBURGER. E., Unserer lieben Frauen Mantel. Eine phylogenetische Studie. Naturw. Wochenschr. 20:49-56. 1905.

<sup>23</sup> WARD, H. MARSHALL, Recent researches on the parasitism of fungi. Ann. of Botany 19:1-54. 1905.

The latter part of the paper is occupied principally with questions brought out by recent discoveries and theories relating to the rusts. It is shown that the uredo stage is probably responsible for the wintering of many rust fungi whose distribution and annual recurrence is not easily explained by the regular alternation of teleuto- and aecidiospores. Specialized races, immunity, susceptibility, and related subjects are discussed. The mycoplasma theory of Eriksson is considered to be without foundation and absolutely erroneous in the light of the speaker's investigations. Students will find this a valuable paper for reference, outlining briefly the main questions that have occupied the minds of investigators at different periods in the development of mycology, while the bibliography of 209 titles is a means of easy access to the literature of the subject.

ERIKSSON<sup>24</sup> also read a brief paper on the vegetative life of the Uredineae. This paper is a review of his mycoplasma theory, mainly as set forth in his former papers.—H. HASSELBRING.

CAMPBELL<sup>25</sup> discusses in detail and combats BOWER's theory that the spike of *Ophioglossum* is the equivalent of a single sporangium of *Lycopodium* and that all pteridophytes are reducible to a common strobiloid type. He repeats his belief, hitherto published, that the progenitor of the large-leaved ferns may have sprung from some bryophyte type, and that the *Ophioglossaceae* may have arisen directly from an *Anthoceros*-like prototype. He regards a species of *Ophioglossum* from Sumatra described by BOWER (Ann. Bot. 18:205. 1904) as nearly realizing the hypothetical form suggested by him as the fern ancestor. The close relationship of the *Ophioglossaceae* and the *Marattiaceae* is pressed upon the grounds of structural resemblances in both gametophyte and sporophyte, and the conclusion is drawn that there is "no valid reason for removing the *Ophioglossaceae* from their association with the ferns." He also reviews the evidence offered by recent writers in regard to the likeness existing between the *Marsiliaceae* and the *Schizaeaceae*. He thinks there is a marked resemblance between the sporocarp of certain of the former group and the fertile leaf segment of *Schizaea*, both as regards structure and the origin of the sporangium. These features combined with "the remarkable correspondence in the structure of the sporangia" he considers sufficient evidence to ally the *Schizaeaceae* and the *Marsiliaceae* not remotely.—FLORENCE LYON.

IN CONTINUATION of his experiments with the *Erysiphaceae* SALMON<sup>26</sup> has established that injury to plants in various ways makes such plants susceptible to biologic forms of *Erysiphe* to which they are normally immune. The fungus

<sup>24</sup> ERIKSSON, J., On the vegetative life of some Uredineae. Ann. of Botany 19:55-60. 1905.

<sup>25</sup> CAMPBELL, D. H., The affinities of the *Ophioglossaceae* and *Marsiliaceae*. American Naturalist 38:761-775. figs. 9. 1904.

<sup>26</sup> SALMON, E. S., Further cultural experiments with "biologic forms" of the *Erysiphaceae*. Ann. of Botany 19:125-148. 1905.

used was the biologic form of *E. graminis* on wheat. This form will not infect rye, but by subjecting rye leaves to various treatments it was found that the fungus could be made to infect this plant also. When leaves of rye were injured either by cutting or bruising or by slugs, the cells around the injured parts could be infected with conidia or ascospores from *E. graminis* on wheat. Other experiments showed that rye leaves subjected to the influence of alcohol, ether, or heat become susceptible to infection from conidia taken from wheat. In some of these cases the fungus produced vigorous growth nearly covering the leaves. Conidia grown on barley in this way retained the power of infecting their original host, but were unable to infect normal untreated leaves of barley. These experiments are especially interesting, since they contribute an experimental proof to the generally current notion that plants of "weakened vitality" are more easily attacked by fungi than vigorous plants. The experiments show that at least in certain cases plants may become more susceptible as a result of injurious agencies affecting the general health of the plant.—H. HASSELBRING.

THE COMPLETED FORM of CLINTON'S<sup>27</sup> monograph of the North American Ustilagineae has recently appeared. This monograph is the result of studies carried on for a series of years at the University of Illinois and completed at Harvard University. The descriptions are based on the author's personal examination of type material so far as this was possible. To the technical descriptions are appended notes of interest giving the distribution of the species, and special characters of aid in separating closely related species. Complete synonymy and references to exsiccata are given, while a bibliography of over 200 titles is found at the end of the volume. A feature of the book is the tabulated list giving the distribution by continents of the species treated in the work. This volume forms an excellent handbook for the study and determination of the smuts of North America. It will prove extremely useful to students and station workers by whom the lack of monographs of groups of parasitic fungi has been long felt. It would have added to the utility of the work to have had the index of hosts arranged alphabetically, with page references for the parasites; instead of classifying the hosts according to orders, which is a time-robbing arrangement.—H. HASSELBRING.

GOEBEL<sup>28</sup> has previously shown that *Bryophyllum crenatum* will develop shoots from the growing region at the margin of the leaves if the midrib be severed, or if all the buds be removed from the shoot. Further studies<sup>29</sup> show that the same result follows if the buds be left intact, but inhibited from growing. All the

<sup>27</sup> CLINTON, G. P., North American Ustilagineae. Proc. Boston Soc. Nat. Hist. 31:329-529. 1904.

<sup>28</sup> GOEBEL, K., Ueber Regeneration im Pflanzenreich. Biol. Centralbl. 22:418. 1902.

<sup>29</sup> GOEBEL, K., Morphologische und biologische Bemerkungen. 14. Weitere Studien über Regeneration. Flora 92:132-146. figs. 6. 1903.



growing points of several shoots were encased in plaster, and after four weeks' time buds appeared along the margin of the leaves. Upon removing the plaster the buds of the shoot continued growing. In this plant the leaf buds arise from already existing growing points. In *Begonia*, however, none of these are present on the leaf, and here also continued removal of the growing point of the shoot resulted in the development of buds on the leaves.

In *Streptocarpus Wendlandi* when the inflorescence is removed a number of the adventitious shoots develop. The interesting feature about these is that they present seedling characters, viz., each has a short shoot-like axis and one large leaf corresponding to the large cotyledon, the opposite leaf being almost invisible or entirely suppressed.—W. B. McCALLUM.

LECLERC DU SABLON<sup>30</sup> finds that the carbohydrate and nitrogenous reserve foods of trees reach their maxima in the autumn, and their minima in May or June after the formation of the leaves and shoots of the season. For carbohydrates the roots are more marked reservoirs than the stems, and the leaves do not function as a storage place. Nitrogenous reserves, however, are more abundant in leaves than in stems or roots, diminishing from spring to autumn, at first very rapidly, then slowly. The stem and roots give up to leaves in process of formation most of their nitrogenous food, and their store is replenished little by little during the season. The fats are scarce in stems or roots; they are more abundant in leaves, in which they increase from spring to autumn. Water is at a maximum in early spring and a minimum in autumn. Autumn, when the water is at a minimum and the reserve food at a maximum, is the most favorable time for the transplantation of trees. SABLON seems to have overlooked some important German work on reserve food in trees, especially that of MUELLER.—C. R. B.

BERTRAND<sup>31</sup> obtained from pure cultures of various orchids the same fungus, and found that the seeds of these species, sowed with this fungus (an *Oospora*?) to the exclusion of other micro-organisms, gave normal plants, regularly infested. *Cypripedium* seeds grown aseptically do not develop; *Cattleya* embryos grow to the spherule stage and no further unless then infected; *Bletia hyacinthina* develops a stem and some leaves, but does not pass this stage unless infected, when it pursues a normal course. The action of the fungus is to incite growth in cells other than those attacked. This knowledge will be useful to growers. In a discussion of tuberization BERTRAND expresses the view that though tuberization is an anomaly of growth (from the morphological point of view) due to an abnormal concentration of the sap, in nature this concentration is brought about not by any of the methods of the laboratory (which have been urged as disproving this theory of tuberization), but by the attacks of endophytic fungi.—C. R. B.

<sup>30</sup> SABLON, LECLERC DU, Recherches physiologiques sur les matières de réserves des arbres. Rev. Gén. Bot. 16:341-368, 386-401. 1904.

<sup>31</sup> BERTRAND, N., Recherches expérimentales sur les Orchidées. Rev. Gén. Bot. 16:458-476. pls. 18-19. 1904.

IT APPEARS from PORODKO's work on the growth of bacteria and molds under different pressures of oxygen,<sup>32</sup> that the maximum pressure of this gas which can be borne varies, in twenty-five organisms studied, from 0.676 to 9.38 atmospheres. A single nutrient medium was used throughout, and the author points out that with other media perhaps the maximal pressures might have been different. The upper limit of oxygen pressure for optimal growth seems not to be related to the maximal pressure. Furthermore, every aerobe has its specific minimal pressure of the gas. This point lies considerably higher for the molds than for bacteria, being about 0.6 atmospheres for *Aspergillus*, *Penicillium*, and *Mucor*, while it is 0.00016 for *Bacillus subtilis*. Of course, in case of facultative anaerobes there is no minimum. The lower limit for most obligate aerobes lies low enough to allow the growth of obligate anaerobes.—B. E. LIVINGSTON.

MISS ROBERTSON,<sup>33</sup> in continuing her study of *Torreya californica*, has described the sexual structures and fertilization. Two to four archegonia are produced, the neck consisting of a single tier of four or six cells. The division of the central cell was observed, and an ephemeral ventral nucleus inferred. The two male nuclei were observed in a common cytoplasmic sheath, but no inequality in the male cells was noted. In fertilization the cytoplasm of the male cell was observed investing the fusion nucleus. In the development of the proembryo wall-formation occurs after four free nuclei have appeared. A count of chromosomes indicated that the reduction number is eight. The general conclusion is reached that the morphological evidence does not bear out the suggestion of cycadean resemblances obtained from the anatomy of the seed and seedling.—J. M. C.

GRÉGOIRE<sup>34</sup> has investigated the reduction of chromosomes in the pollen mother-cells of *Lilium speciosum* and *Allium fistulosum*. The immediate occasion for the investigation was that STRASBURGER's recent conclusions<sup>35</sup> conflict with those of BERGHS,<sup>36</sup> a pupil of GRÉGOIRE. The present investigation convinces GRÉGOIRE that his pupil is correct in his interpretations, and that STRASBURGER's recent interpretation of mitosis in *Thalictrum purpurascens* will not apply to *Lilium*, *Allium*, and *Convallaria*. The most interesting observation in the present paper concerns alternations of generation. GRÉGOIRE claims that since reduction is not complete until the four spores are formed from the

<sup>32</sup> PORODKO, THEODOR, Studien über den Einfluss der Sauerstoffspannung auf pflanzliche Mikroorganismen. Jahrb. Wiss. Bot. 41:1-64. 1904.

<sup>33</sup> ROBERTSON, AGNES, Studies in the morphology of *Torreya californica*. II. The sexual organs and fertilization. New Phytol. 3:205-216. pls. 7-9. 1904.

<sup>34</sup> GRÉGOIRE, VICTOR, La réduction numérique des chromosomes et les cinèses de maturation. La Cellule 21:297-314. 1904.

<sup>35</sup> STRASBURGER, EDUARD, Ueber Reduktionsteilung. Sitzungsber. K. K. Preuss. Akad. Wiss. 18:—, [1-28.] 1904. See BOT. GAZETTE 38:397-398. 1904.

<sup>36</sup> BERGHS, JULES, La formation des chromosomes hétérotypiques dans la sporogénèse végétale I. La Cellule 21:173-189. 1904. See BOT. GAZETTE 38:228. 1904.

mother-cell, the gametophytic generation begins with the spore rather than with the spore mother-cell.—CHARLES J. CHAMBERLAIN.

BORGESSEN and JENSEN<sup>37</sup> have given a floristic description of a portion of heath in Jutland, Denmark. On the suggestion of WARMING, a part of the estate now meadow has been reserved for experimental purposes, the object being to trace the developmental phases from cultivated soil to heath. Another portion of the heath was burned over in order to trace the progressive stages from no vegetation until the tract is again converted into the *Calluna* heath. Another object in view is to trace the succession of plants on areas which now are or are to be planted with conifers. The data of the present condition seem to be thoroughly detailed and classified. Hence it would seem that future observations on this tract will furnish interesting and valuable material for the ecologist.—G. H. JENSEN.

STOKLASA<sup>38</sup> reports the finding of lactic acid produced by the enzyme lactolase as one of the intermediate products of anaerobic respiration of gourds, beets, and potatoes, under aseptic conditions. Acetic acid and formic acids were also formed. Meanwhile BUCHNER has abandoned his contention that lactic acid is one of the intermediate products in alcoholic fermentation (with which STOKLASA absolutely identified anaerobic respiration), in the light of the researches of NEF. At the close of his paper STOKLASA hints darkly at results which indicate that chlorophyll-free plant cells form  $\text{CHOH}$  as in photosynthesis, the  $\text{CO}_2$  being reduced by nascent H to formaldehyde, water being again formed.—C. R. B.

LIVINGSTON finds<sup>39</sup> that the cations of many metallic nitrates and sulfates act in the same way and at the same concentration upon *Stigeoclonium*, producing death at certain concentrations, causing the filamentous form to become palmelloid at lower concentrations, and sometimes at the latter concentrations, but oftener at a still lower one, accelerating in a marked degree the formation of zoospores. The palmella effect is identical with that produced by withdrawal of water, but the zoospore effect is exactly the opposite. The degree of toxicity of the metals found agrees in a general way with that found by other observers, though there are many unexplained discrepancies.—C. R. B.

ON THE BASIS of comparative researches with the quartz spectrograph, TSCHIRCH comes to the conclusion<sup>40</sup> that the yellow pigments of flowers and

<sup>37</sup> BORGESSEN, —, and JENSEN, —, En floristisk Undersøgelse af et Stykke Hede i Vestjylland. (A floristic research on a portion of heath in West Jutland.) Bot. Tidsskrift 26: ——. 1904.

<sup>38</sup> STOKLASA, J., Ueber das Enzym Lactolase, welches die Milchsäurebildung in der Pflanzenzelle verursacht. Ber. Deutsch. Bot. Gesells. 22:460-466. 1904.

<sup>39</sup> LIVINGSTON, B. E., Chemical stimulation of a green alga. Bull. Torr. Bot. Club 32:1-34. figs. 17. 1905.

<sup>40</sup> TSCHIRCH, A., Vergleichend-spektralanalytische Untersuchungen, etc. Ber. Deutsch. Bot. Gesells. 22:414-439. 1904.

fruits betray no close relationship with artificial yellow pigments, a large number of both being investigated. Rather the plant pigments show alliances with the phytosterins. Carotin, he adds, probably is allied to THIELE's *fulvin*, and its chromatophore radicles contain a quinate ring of which at least three C-atoms have double bonds.—C. R. B.

VUILLEMIN<sup>41</sup> has published a paper on the development and structure of the membrane of the zygospore in the mucors. The main contribution of the paper is the recognition of the fact that the membrane is more complex than has usually been supposed. The author distinguished five distinct layers which differentiate successively and differ from each other in thickness, appearance, and in their behavior toward reagents. The study includes *Sporodinia*, *Spinellus*, *Zygorhynchus*, and *Mucor*.—H. HASSELBRING.

AN INVESTIGATION under the direction of PALLADIN by L. PETRASCHESKY<sup>42</sup> shows that when *Chlorothecium saccharophilum* is fed with raffinose its respiratory quotient in anaerobic life is raised much above 1 (in aerobic life it is 0.74–0.89), while with maltose it falls below the normal. Acids are probably produced as decomposition products in the former case and alcohol-like substances in the latter.—C. R. B.

CULTIVATION in a greenhouse modifies notably the external form, the habit, and the structure of plants, according to the experimental studies of BÉDÉLIAN.<sup>43</sup> This he ascribes to the humidity, nearly uniform temperature, and the weaker diffuse light. In general differentiation is more or less arrested, and there are manifested various adaptations to the new conditions.—C. R. B.

FRIEDEL finds the effect of insufficient oxygen on the anatomy of certain plants quite parallel with that of darkness. The relative thickness of the cortex is increased, that of the pericyclic region is diminished, and lignification is incomplete.<sup>44</sup> The experiments, however, cannot be continued long enough to make these effects as marked as in etiolation.—C. R. B.

KELLCOTT<sup>45</sup> finds in roots of *Allium* and *Podophyllum* two maxima (c. 11 and 1 P. M.) and two minima (c. 7 A. M. and 3 P. M.) in cell division, which are not affected by slight variations in temperature, but are affected by solutes in tap water. Elongation maxima and minima in *Allium* coincide respectively with minima and maxima in cell division.—C. R. B.

<sup>41</sup> VUILLEMIN, P., Recherches morphologiques et morphogéniques sur la membrane des zygospores. *Ann. Mycol.* 2:483–506. pls. 8–11. 1904.

<sup>42</sup> PETRASCHESKY, L., Ueber Atmungskoeffizienten der einzelligen Alge *Chlorothecium saccharophilum*. *Ber. Deutsch. Bot. Gesells.* 22:323–327. 1904.

<sup>43</sup> BÉDÉLIAN, J., Influence de la culture en serre sur quelques plantes des environs de Paris. *Rev. Gén. Bot.* 16:318–336. pls. 10–13. 1904.

<sup>44</sup> FRIEDEL, JEAN, Influence d'une faible pression d'oxygène sur la structure anatomique des plantes. *Rev. Gén. Bot.* 16:305–317. 1904.

<sup>45</sup> KELLCOTT, WM. E., The daily periodicity of cell division and of elongation in the root of *Allium*. *Bull. Torr. Bot. Club* 31:529–550. figs. 8. 1904.

## NEWS.

DR. G. BITTER, formerly of the University of Münster, has been appointed director of the recently established Botanical Garden at Bremen.

DR. W. MIGULA, formerly at the Technical School at Carlsruhe, has been appointed professor of botany at the School of Forestry at Eisenbach.

PROFESSOR CHARLES R. BARNES, University of Chicago, sailed for Europe April 8, to be absent seven months. He will attend the International Botanical Congress at Vienna.

THE CEDAR POINT LAKE LABORATORY of the Ohio State University offers instruction in general botany and ecology from June 26 to August 4. The instructor is OTTO E. JENNINGS, Carnegie Museum.

AT THE THIRD ANNUAL MEETING of the Central Branch of American Society of Naturalists and Affiliated Societies, held at Chicago March 31 and April 1, the annual address of the chairman, PROFESSOR JOHN M. COULTER, University of Chicago, was upon "Public interest in research."

THE MARINE BIOLOGICAL LABORATORY at Woods Hole, Mass., offers instruction in Thallophtyes and Cell studies from June 28 to August 9, 1905. The instructors are BRADLEY MOORE DAVIS, University of Chicago; JAMES J. WOLFE, Trinity College, N. C., and ROBERT B. WYLIE, Morningside College, Iowa.

THE BOTANICAL SOCIETY of the Netherlands has begun the publication of its *Archives* in two parts. The title of one is *Nederlandsch Kruidkundig Archief*, dealing with the Dutch flora and printed in Dutch; that of the other is *Recueil des travaux botaniques Néerlandais*, dealing with subjects of more general interest.

THE BERMUDA BIOLOGICAL STATION FOR RESEARCH will be open in 1905 under the direction of Professor E. L. MARK, of Harvard University, and Professor C. L. BRISTOL, of New York University. Botanists who wish to take advantage of the station must apply not later than May 1. The date of sailing from New York is July 1 and six weeks will be spent at the station.

WITH ITS January number the *Indian Forester* commences its thirty-first volume with a great improvement in appearance. In typography, size, and contents the subscription price (12s 6d) is exceedingly low. While the journal devotes considerable space to the discussion of forest problems that confront the Forest Service in India, it discusses problems of much wider scope and is of general interest to all students of forestry.

THE AMERICAN MYCOLOGICAL SOCIETY met in affiliation with the A. A. A. S. at Philadelphia, December 28 to 31. The following officers were elected: President, CHARLES H. PECK; Vice-President, F. S. EARLE; Secretary-treasurer, C. L. SHEAR; and the following committee on organization and relation to the other societies was appointed: C. L. SHEAR, S. M. TRACY, and ROLAND THAXTER. The following program was presented: Suggestions for the study of dairy fungi, CHARLES THOM; A new disease of the cultivated agave, GEORGE G. HEDGCOCK; A study of North American Coleosporiaceae, and The terminology of the spore-structures in the Uredinales, J. C. ARTHUR; Classification of the Geoglossaceae, E. J. DURAND; Generic characters of North American Thelephoraceae, E. A. BURT; Cultures of wood-inhabiting fungi, PERLEY SPAULDING; Two fungous parasites on mushrooms, and The genus *Balansia* in the United States, G. F. ATKINSON.

THE "BOTANISTS of the Central States" met at the University of Chicago, March 31 and April 1, in connection with the Central Branch of the American Society of Naturalists, with STANLEY COULTER, of Purdue University, as chairman, and CHAS. F. MILLSAUGH, of the Field Columbian Museum, as secretary. The following papers were read and discussed:

C. F. HOTTES, University of Illinois, The effect of starvation on the cells of the root tip; W. B. MCCALLUM, University of Chicago, Regeneration and polarity in the higher plants; R. H. POND, Northwestern University, The endosperm enzyme of *Phoenix dactylifera*; E. W. OLIVE, University of Wisconsin, Nuclear and cell division in certain lower plants; E. O. JORDAN, University of Chicago, A rosette-forming micro-organism; F. M. LYON, University of Chicago, Development of the megaspore coats of *Selaginella*; R. A. HARPER, University of Wisconsin, The nuclear fusion in the ascus, and alternation of generations in the Ascomycetes; A. H. CHRISTMAN, University of Wisconsin, Sexual reproduction in the rusts; B. M. DAVIS, University of Chicago, The sexual organs of the Rhodophyceae and Uredinales; C. J. CHAMBERLAIN, University of Chicago, Apogamy and apospory in ferns; E. B. SIMONS, University of Chicago, The morphology and development of the conceptacle in *Sargassum*; J. B. OVERTON, University of Wisconsin, The permanence of the chromosomes and their behavior in synapsis; C. F. MILLSAUGH, Field Columbian Museum, Recent field-work in the Bahamas.

A permanent organization of the society was effected, with WILLIAM TRELEASE, Missouri Botanic Garden, as president, and H. C. COWLES, University of Chicago, as secretary-treasurer.

# BOTANICAL GAZETTE

MAY, 1905

## ON PROTEOLYTIC ENZYMES. I.

ARTHUR L. DEAN.

NUMEROUS investigators have studied the proteolytic enzymes in plants and their work appears to have been carried on from two different points of view. The physiological chemists working with vegetable proteases have made careful studies of the products and nature of the action of enzymes of marked activity. Of such work, the investigations carried on by CHITTENDEN and his pupils on bromelin are excellent examples. In studies of this kind the enzyme is the important thing, the rôle of the enzyme in the physiology of the plant is secondary. On the other hand, the studies of plant physiologists have been directed less to working out the nature of the enzymes and more to locating them and to discovering their function in the life of the plant. Of such researches the intensive studies of BUTKEWITSCH on germinating seeds, and the extensive ones of VINES on all sorts of plant tissues, are good illustrations.

Looking at the subject from the point of view of plant physiology, we may conceive of proteolytic enzymes as being digestive, *i. e.*, acting on stores of proteid, as in germinating seeds; or metabolic, *i. e.*, acting on the proteids in the life of the vegetable cells. The idea of enzymes digesting the reserve proteids was the first to occur to physiologists. Acting on the hypothesis of the existence of such enzymes, numerous investigators have examined germinating seeds, using a variety of methods, and obtaining results which have not always been in harmony with the hypothesis or with each other.

The view that wherever we find proteids in an organism, there we should always find a proteolytic enzyme, is not a new one; the experimental facts to support such a conception have been slow

in coming. Manifestly the first step in proving this assumption is to show that proteolytic enzymes are present in all parts of all living plants, or to demonstrate their presence in a sufficient number of places to warrant the conclusion that they are universally present. Such extensive researches have not been undertaken until the last few years.

I shall briefly review the results of the various investigations, taking first the studies on the digestive enzymes, as I have called them, and then those on the metabolic enzymes.

GORUP-BESANÉZ<sup>1</sup> appears to have been the first to examine seeds for proteolytic enzymes. Using the Wittich glycerin method he obtained protease preparations from the resting seeds of hemp, flax, and vetch, and from the germinating barley; he failed to find enzymes in ungerminated barley, lupin seeds, *Secale cornutum*, pine, and corn, and in seedlings of almonds and beans.

VAN DER HARST<sup>2</sup> found that a glycerin extract of the cotyledons of germinating beans would digest fibrin.

The first careful study of a seed proteolytic enzyme was that of J. REYNOLDS GREEN<sup>3</sup> who investigated the germinating seeds of *Lupinus hirsutus*. GREEN's results showed conclusively that these plants contain an active enzyme, capable of attacking fibrin, as well as the proteids of the seeds themselves. The enzyme was not present in the resting seeds. Later GREEN discovered a similar enzyme in the seedlings of the castor oil bean.<sup>4</sup>

NEUMEISTER<sup>5</sup> undertook the study of a number of seeds and seedlings, using a method different from that of any previous investigator in this field. Pieces of fibrin were soaked in the watery extracts from the tissues to be tested; subsequently the fibrin was transferred to a weakly acid solution and allowed to digest. In case a proteolytic enzyme was present it was taken up by the fibrin, and in the acid medium proteolysis of the fibrin took place. The value

<sup>1</sup> GORUP-BESANEZ, Ber. Deutsch. Chem. Gesells. 7:1478. 1874; 8:1510. 1875; and 9:673. 1876.

<sup>2</sup> VAN DER HARST, Moonblad voor Naturwetensch. 1867, Sept. 20.

<sup>3</sup> GREEN, J. REYNOLDS, Phil. Trans. 178:(B) 39. 1887.

<sup>4</sup> GREEN, J. REYNOLDS, Proc. Roy. Soc. 48:370. 1890.

<sup>5</sup> NEUMEISTER, Zeitschr. für Biologie 30:447. 1894.



of the negative results by this method has been called in question by FRANKFURT.<sup>6</sup> NEUMEISTER's results may be summarized as follows:

## POSITIVE RESULTS

Barley seedlings—sprouts 3<sup>cm</sup> long.  
 Barley seedlings—sprouts 5<sup>cm</sup> long.  
 Barley seedlings—sprouts 15–20<sup>cm</sup> long.  
 Poppy seedlings.  
 Beet seedlings.  
 Corn seedlings—sprouts 10<sup>cm</sup> long.  
 Corn seedlings—sprouts 16<sup>cm</sup> long.  
 Wheat seedlings—sprouts 17<sup>cm</sup> long.

## NEGATIVE RESULTS

Barley seeds.  
 Barley seedlings—sprouts 0.5 to 1<sup>cm</sup>.  
 Poppy seeds.  
 Beet seeds.  
 Corn seeds.  
 Lupin seeds.  
 Lupin seedlings—sprouts 3<sup>cm</sup>.  
 Lupin seedlings—sprouts 12<sup>cm</sup>.  
 Lupin seedlings—sprouts 20<sup>cm</sup>.  
 Vicia seeds.  
 Vicia seedlings.  
 Pea seeds.  
 Pea seedlings.  
 Rye seeds.  
 Rye seedlings.  
 Oat seeds.  
 Oat seedlings.

A number of different investigators have worked on malt; the evidence shows that the germinating barley contains a proteolytic enzyme. WEISS<sup>7</sup> thinks there are two, a peptic and a tryptic enzyme, a view which is supported by FERNBACH and HUBERT,<sup>8</sup> but questioned by VINES.

In the course of the extensive studies of FERMI and BUSCALIONI<sup>9</sup> on proteases in plants, they tested a number of seeds and found that the ripe seeds of several plants contain an enzyme capable of liquefying gelatin. They likewise found that the germinating seeds of some plants contained such enzymes, but in other cases no evidence of their presence could be found.

BUTKEWITSCH<sup>10</sup> made a careful study of the germinating seeds of two lupins, *L. angustifolius* and *L. luteus*, and a somewhat shorter

<sup>6</sup> FRANKFURT, Landw. Versuchsstat. 47:466. 1896.

<sup>7</sup> WEISS, Zeitschr. für Physiol. Chem. 31:79.

<sup>8</sup> FERNBACH and HUBERT, Compt. Rend. 130:1783.

<sup>9</sup> FERMI and BUSCALIONI, Centralbl. Bact., etc. II. 5:24. 1899.

<sup>10</sup> BUTKEWITSCH, Zeitschr. Physiol.-Chem. 32:1. 1901.

examination of *Ricinus major* and *Vicia Faba*. His experiments show that the proteids in the sprouting seeds of all these species will undergo autolysis, giving rise to products not precipitable by phosphotungstic acid. From *L. luteus* he made a proteid preparation by the Wittich method (solution in glycerin and precipitation by alcohol) which acted on "conglutin" with the formation of leucin and tyrosin, but not of asparagin.

VINES<sup>11</sup> found some difficulty in getting a formation of tryptophan in the autolysis of germinating seeds of *Vicia Faba*; the reaction was readily obtained, however, if Witte peptone was added to the mixture and digestion allowed to proceed. He found that the embryo of the wheat contains an enzyme which readily attacks Witte peptone and apparently has some slight action on some of the proteids of the embryo.

As stated above, the first step in demonstrating that proteases are universally at work where proteids occur, is to show that all living plant tissues contain proteolytic enzymes. Investigations of this sort have been undertaken but recently. The older researches, which did not have this purpose, did tend to show that active proteases occur in places other than germinating seeds. The papain of the pawpaw fruit, the bromelin of the pineapple juice, the cradein of the latex and juice of the fruit of the fig, and the protease of the Kachree gourd and of *Anagallis arvensis* have been known for some time, but these plants were looked upon as exceptional.

FERMI and BUSCALIONI<sup>12</sup> were the first to make a systematic examination of a large number of plant tissues. Their method consisted in placing the objects to be tested on gelatin containing phenol as an antiseptic. If the gelatin was liquefied by the tissue or tissue extract, a protease was judged to be present. The positive results of this method are valuable; negative results cannot be taken as conclusive evidence that no proteolytic enzyme is present, since all proteases do not attack gelatin, and phenol is said to have an inhibitory influence on the action of some enzymes. These investigators succeeded in showing that proteases occur in a great diversity of plants and of plant parts. Their negative results are sufficiently numerous

<sup>11</sup> VINES, Annals of Botany 16:12. 1902.

<sup>12</sup> FERMI and BUSCALIONI, Centralbl. Bact., etc., II. 5:24. 1899.

to cause some doubt in respect to the universal occurrence of proteases in living tissues, and the positive results were obtained with such a diversity of tissues that they do not lead to any definite hypothesis of the physiological rôle of these enzymes. In view of the evidence of VINES' researches, it appears probable that a more thorough study of the tissues examined by FERMI and BUSCALIONI would show that proteases are present there which cannot act under the conditions of their experiments. Their positive results support the theory of the universal distribution of proteolytic enzymes, their negative results do not disprove it.

Finally we come to a consideration of the results of VINES.<sup>13</sup> He believes that all vegetable proteases are proteolytic in distinction from peptonizing, *i. e.*, that they change the proteids which they attack into their ultimate cleavage products, amido-acids, hexon bases, etc., and do not stop, like pepsin, with the albumoses and peptones in preponderance. Acting on this well-justified assumption, he expects to find tryptophan as the result of the action of vegetable proteases, and uses as a test for proteolysis the progressive formation of tryptophan as shown by the color reaction with chlorine or bromine water. He uses the method of autolysis, allowing the enzymes of a tissue to digest the proteids of that tissue and from time to time tests samples of the mixture for tryptophan. He frequently adds other proteids to the digestion, especially Witte peptone. The only objection to the method is that some proteids do not contain the tryptophan group, or only a small amount of it. A negative result by VINES' method with a tissue containing such a proteid would not mean much. This probably explains the differences between the results obtained by VINES and BUTKEWITSCH in their examinations of the germinating seeds of *Vicia Faba*, since OSBORNE and HARRIS<sup>14</sup> have shown that the proteids of this seed give but a faint Adamkiewicz reaction, a reaction which HOPKINS and COLE<sup>15</sup> have shown to be due to the presence of the tryptophan group in the proteid molecule. By using Witte peptone, VINES obtains evidence of proteolysis in cases where the tissue contains

<sup>13</sup> VINES, *Annals of Botany* 16:1. 1902; 17:237 and 597. 1903; and 18:289. 1904.

<sup>14</sup> OSBORNE and HARRIS, *Jour. Am. Chem. Soc.* 25:853. 1903.

<sup>15</sup> HOPKINS and COLE, *Jour. Physiology* 27:419. 1901.

no peptonizing enzyme, but does have an enzyme which, like erepsin of the animal body, attacks albumoses and peptones. In cases where all the trials were made with the addition of Witte peptone, it is impossible to say whether there is an enzyme present of the trypsin type (tryptase), the erepsin type (ereptase), or both. In cases where a positive result was obtained both with or without the addition of Witte peptone, a tryptase is present if, as is probable, the tissue contains no marked quantity of albumoses or peptones; an ereptase may also be present and in the table its presence is indicated as questionable. When no tryptophan reaction is given on autolysis, except after the addition of a proteose, I have assumed that no tryptase was present, an assumption which, as pointed out above, is not entirely justified because certain proteids give no reaction for the tryptophan radical (see table).

This table records but three failures to obtain evidence of a protease, the pulp of the apple, the juice of the orange, and the sap of the bleeding birch tree (*Betula alba*), which last is not a cell extract. The two failures, the apple and the orange juice, are scarcely sufficient to prevent the acceptance of these results as evidence of the universal occurrence of proteases in living plant tissues.

No mention has been made of the proteolytic enzymes of the insectivorous plants and the bacteria and lower fungi. Some of the latter are doubtless endo-enzymes and belong to the group which I have termed metabolic enzymes. The others are apparently secretions designed to render food materials available and should be classed with the digestive enzymes.

The results of VINES tend to show that there are enzymes of the erepsin type widely distributed in plants, yet the evidence is not wholly conclusive and he has made no attempt to isolate such enzymes. DELEZENNE and MOUTON<sup>16</sup> made extracts from several fleshy fungi, *Amanita muscaria*, *Amanita citrina*, *Hypholoma fasciculare*, and *Psalliota (Agaricus) campestris*, which were judged to contain an ereptase since they digested proteoses but not fibrin. VINES finds, however, that *Agaricus campestris*, which DELEZENNE and MOUTON found to yield an especially active ereptase, is capable of autolysis and will digest fibrin if the fibrin is not boiled. The unboiled fibrin

<sup>16</sup> DELEZENNE and MOUTON, Compt. Rend., April 9, 1903.

Tissue	Tryp- tase	Erep- tase	Erep- tase or Tryp- tase or both
Milk of <i>Cocos nucifera</i> .....	—	+	..
Pilei of <i>Agaricus campestris</i> .....	+	++?	..
Unripe seeds of <i>Pisum sativum</i> .....	+	++?	..
Fruit of <i>Cucumis melo</i> .....	+	++?	..
Fruit of <i>Cucumis sativus</i> .....	+	++?	..
Fruit of <i>Cucurbita pepo-ovifera</i> .....	..	..	+
Fruit of <i>Ecballium Elaterium</i> .....	—	+	..
Fruit of <i>Musa sapientum</i> .....	+	++?	..
Fruit of <i>Lycopersicum esculentum</i> .....	+	++?	..
Fruit of <i>Pyrus malus</i> (pulp).....	—	—	—
Fruit of <i>Pyrus malus</i> (skin).....	—	+	..
Fruit of <i>Pyrus communis</i> .....	—	+	..
Fruit of <i>Citrus aurantium</i> (juice).....	—	—	—
Fruit of <i>Citrus aurantium</i> (peel).....	?	+	..
Fruit of <i>Vitis vinifera</i> .....	..	..	+
Sap of <i>Betula alba</i> .....	—	—	—
Shoots of <i>Crambe maritima</i> .....	—?	+	..
Yeast.....	+	++?	..
Latex of <i>Euphorbia Characias</i> .....	—	+	..
Latex of <i>Lactuca sativa</i> .....	—?	+	..
Stems of <i>Dahlia variabilis</i> .....	—	+	..
Stems of <i>Cucurbita pepo-ovifera</i> .....	+	++?	..
Stems of <i>Mirabilis Jalapa</i> .....	+	++?	..
Stems of <i>Helianthus tuberosus</i> .....	+	++?	..
Stems of <i>Cuscuta</i> .....	—	+	..
Leaves of <i>Spinacia oleracea</i> .....	+	++?	..
Leaves of <i>Dahlia variabilis</i> .....	+	++?	..
Leaves of <i>Tropaeolum majus</i> .....	+	++?	..
Leaves of six other species of plants.....	+	++?	..
Leaves of <i>Holcus mollis</i> and three other species of plants.....	..	..	+
Bulbs of <i>Tulipa</i> and two other plants.....	+	++?	..
Tubers of <i>Solanum tuberosum</i> .....	+	.....	.....
Tubers of <i>Helianthus tuberosus</i> .....	+	++?	..
Roots of <i>Dahlia variabilis</i> .....	+	++?	..
Roots of <i>Brassica Rapa</i> and seven other plants.....	—	+	..

which VINES used would not digest itself and he believes its solution was not due to any enzyme which the fibrin itself contained. VINES agrees with DELEZENNE and MOUTON in believing that this fungus contains an enzyme of the erepsin type.

#### EXPERIMENTAL DATA

In undertaking the study of the proteolytic enzymes I have had two ends in view. In the first place it was thought desirable to test a number of different plant tissues in order to confirm, if possible, the results of VINES. The second and more important part of the investigation was to make a careful study of the enzymes in some

one or two plants, tracing their occurrence and studying their nature throughout the life history of the plant. In this way it was hoped that some results might be obtained which would throw light on the nature and functions of the proteases in the life of plants. For this study the common field bean, *Phaseolus vulgaris*, which has a large proteid content in its seeds and shows marked vigor and rapidity in its growth, was selected. The work on the enzymes of *Phaseolus* has proved so absorbing that scant attention has been paid to the testing of various plants. The few positive results which have been obtained will be set down at this time.

**SPINACIA OLERACEA.**—Fresh leaves of spinach were carefully picked over to remove all imperfect tissue and then ground up and the juice removed by a screw press. The residue was rubbed up with a little water and the fluid again pressed out. The turbid dark green extract was examined as follows:

Flask no. 1—50°c extract—boiled.

Flask no. 2—50°c extract—unboiled.

Flask no. 3—50°c extract + .5 gm Witte peptone—boiled.

Flask no. 4—50°c extract + .5 gm Witte peptone—unboiled.

Flask no. 5—50°c extract + .5 gm Witte peptone + 0.25 gm citric acid—boiled.

Flask no. 6—50°c extract + .5 gm Witte peptone + 0.25 gm citric acid—unboiled.

The antiseptic was chloroform, the length of digestion 30 hours. Ten cubic centimeters of each digestion were tested by acidifying with acetic acid, drying, taking up in alcohol and filtering off the residue, drying the alcoholic extract, taking up the residue in water, and applying the tryptophan test with chlorine water. The results were negative except in the case of no. 4, which showed a fair tryptophan reaction. This result shows that the leaves of spinach contain an enzyme capable of attacking Witte peptone, but not acting on the proteids of the tissue, or if it does these proteids do not yield tryptophan on hydrolysis.

**BRASSICA OLERACEA.**—The leaves of a half-matured cabbage, some of which were green and some etiolated, were run through a chopping machine and the pulp macerated with water. The fluid was removed by a screw press and the pale green turbid extract filtered. This extract was faintly acid to litmus, but not to lacmoid, and yielded a coagulum on boiling, the filtrate from

which gave a faint tryptophan reaction. The extract was examined in the following way:

Flask no. 1—50<sup>cc</sup> extract.

Flask no. 2—50<sup>cc</sup> extract—boiled.

Flask no. 3—50<sup>cc</sup> extract + 1<sup>cc</sup> 4 per cent. HCN

Flask no. 4—50<sup>cc</sup> extract + 1<sup>cc</sup> 4 per cent. HCN—boiled.

Flask no. 5—50<sup>cc</sup> extract + 1<sup>cc</sup> 4 per cent. HCN + 0.5 <sup>gm</sup> Witte peptone.

Flask no. 6—50<sup>cc</sup> extract + 1<sup>cc</sup> 4 per cent. HCN + 0.5 <sup>gm</sup> Witte peptone—boiled.

Flask no. 7—50<sup>cc</sup> extract + 0.25 Na<sub>2</sub> CO<sub>3</sub>.

Flask no. 8—50<sup>cc</sup> extract + 0.25 Na<sub>2</sub> CO<sub>3</sub>—boiled.

Ten drops of toluol were added to nos. 1, 2, 7, and 8. The flasks were corked and placed in the incubator. After twenty hours' digestion 10<sup>cc</sup> was removed from each flask, boiled, filtered, and 1<sup>cc</sup> of acetic acid added to each filtrate. The tryptophan test with chlorine water showed that proteolysis had taken place in all the unboiled digestions except no. 3; that in no. 1 was feeble compared with the action in nos. 5 and 7. These results show that although the enzymes of the cabbage leaves act on the proteids of the tissue, yet that action is slight compared with that exerted upon Witte peptone. The tissue residue from which the extract had been obtained was shaken up with water and toluol, a small portion removed and boiled, and Witte peptone added to both parts. After two days' digestion a sample of the fluid in each flask was tested for tryptophan; the unboiled digestion gave a strong reaction, the boiled one a very faint reaction. The fluid was removed as far as possible from the unboiled digestion mixture, concentrated to a syrup, treated with several volumes of alcohol to remove the proteoses and peptones, and the filtrate concentrated to a thick syrup. After standing, very characteristic crystals of both leucin and tyrosin separated.

DAUCUS CAROTA.—Blossoms of the wild carrot were ground in a mortar with water. The mashed tissue and water were divided into four parts and placed in test tubes.

Tube no. 1—tissue + H<sub>2</sub>O + toluol + uncoagulated egg albumen.

Tube no. 2—tissue + H<sub>2</sub>O + toluol + uncoagulated egg albumen—boiled.

Tube no. 3—tissue + H<sub>2</sub>O + Witte peptone + toluol.

Tube no. 4—tissue + H<sub>2</sub>O + Witte peptone + toluol—boiled.

The egg albumen was added because a test of the tissues with

Adamkiewicz reaction, using glyoxylic acid and concentrated sulphuric acid, gave no well-defined positive result. After two days, digestion no. 3 was found to give a weak tryptophan reaction, whereas none of the others gave a positive result. An experiment carried out in the same way with the developing seeds gave the same result except that the unboiled test with Witte peptone gave a much stronger reaction for tryptophan, showing that the proteolysis had been more vigorous. The evidence indicates that the enzyme present is an ereptase.

*CASTANEA SATIVA AMERICANA*.—The leaves of this tree were ground with sand in a mortar, the pulp mixed with water, divided between four test tubes, and examined as follows:

- No. 1—toluol + uncoagulated egg albumen.
- No. 2—toluol + uncoagulated egg albumen—boiled.
- No. 3—toluol + Witte peptone
- No. 4—toluol + Witte peptone—boiled.

After two days in the incubator no. 3 gave a faint reaction for tryptophan, the others none. The original pulp from the leaves gave no Adamkiewicz reaction. The unripe seeds of the chestnut were ground to a paste and mixed with water. No Adamkiewicz reaction was given by this mixture, which was divided between four test tubes and examined in precisely the same way as the leaves. The result was qualitatively the same, but the tryptophan reaction in the unboiled trial with Witte peptone was very strong, showing the presence of an active protease, probably an ereptase.

*PHASEOLUS MUNGO*.—Three weeks old etiolated seedlings of this bean were rubbed up in a mortar and covered with glycerin and a little toluol. After extracting for twenty-two hours, the glycerin was somewhat diluted, strained through gauze, and filtered through absorbent cotton. This extract was tested as follows:

- No. 1—10<sup>cc</sup> extract + fibrin.
- No. 2—10<sup>cc</sup> extract boiled + fibrin.
- No. 3—10<sup>cc</sup> extract + Witte peptone.
- No. 4—10<sup>cc</sup> extract + Witte peptone—boiled.

Examined after three days' digestion no. 1 showed no digestion of the fibrin and gave no test for tryptophan, no. 3 gave a marked tryptophan reaction, and no. 4 none.



**CUCURBITA MAXIMA.**—The seeds of this plant and the young seedlings with radicles an inch and a half long were found to contain an ereptase of considerable power as shown by the action of their tissues on Witte peptone. Under conditions for autolysis none seemed to take place, since no tryptophan reaction was obtainable, notwithstanding the fact that the proteids of this seed give a strong Adamkiewicz reaction. When the seedlings were thirteen days old, however, they were found capable of autolysis with the formation of tryptophan. The results show that the seeds contain an ereptase and that after germination has proceeded for some time a tryptase also makes its appearance.

**CUCURBITA PEPO.**—The seeds of the pumpkin give the same evidence of the presence of an ereptase as do those of the Hubbard squash. Two attempts were made to obtain preparations of this enzyme. A quantity of ground seeds of the pumpkin were whipped up in water, and the shells, which floated on the surface, were skimmed off. After extracting for several hours, the mixture was strained through gauze and an attempt made to filter it clear. The fluid appeared to have a quantity of emulsified fat in it, and even the repeated filtration through pulp filters failed to make any impression on it. The mixture was allowed to stand two days with toluol to prevent bacterial action and was then readily filtered, yielding a perfectly clear filtrate, which however possessed no proteolytic power. In the second attempt 45<sup>gm</sup> of ground seeds were extracted with sufficient water to make 275<sup>cc</sup> of milky looking extract which was found to have a marked action on Witte peptone. As soon as this extract was strained from the ground seeds it was mixed with an equal volume of saturated ammonium sulphate solution and allowed to stand over night. The precipitate was filtered off the next day, and when tested with Witte peptone was found to be very active, showing that the enzyme is either precipitated by half saturation of its solution with ammonium sulphate, or else it sticks to the proteid precipitated by the salt. The precipitate was whipped up in water, transferred to a parchment paper bag, and dialyzed for two days in running water. When taken from the dialyzer and filtered clear, the solution was found to be inactive on Witte peptone. These results show that this enzyme is very sensitive and that some

other means must be resorted to in order to obtain preparations of it free from the bulk of proteids, etc., in the tissue extracts.

#### STUDY OF THE PROTEASES OF PHASEOLUS VULGARIS

The beans used in the experiments to be described were of two sorts, the red kidney bean and the white medium field bean; there has been nothing to suggest that the proteases in these varieties are different, and in the records of experiments no mention will be made of which kind was used.

*Resting seeds.*—The resting seeds were tested a number of times for proteases; the results always showed that the seeds contained an enzyme capable of hydrolyzing Witte peptone with the formation of tryptophan, but incapable of digesting the phaseolin of the seed. Later in this paper will be found a more detailed description of this ereptase. The record of a typical experiment is given here.

Seeds of *Phaseolus vulgaris* which were known to germinate readily were ground to a fine meal, one gram of this powder placed in each of four test tubes, and further additions made as follows:

No. 1—15<sup>cc</sup> H<sub>2</sub>O + toluol.

No. 2—15<sup>cc</sup> H<sub>2</sub>O + toluol—boiled.

No. 3—15<sup>cc</sup> H<sub>2</sub>O + toluol + 0.3<sup>gm</sup> Witte peptone.

No. 4—15<sup>cc</sup> H<sub>2</sub>O + toluol + 0.3<sup>gm</sup> Witte peptone—boiled.

All were corked, shaken, and kept in the incubator at 37–39° C. for forty-one hours. At the expiration of that time the contents of each tube were boiled, acidified with acetic acid, and filtered. The filtrates were then tested.

No. 1—no biuret, Millon's, nor tryptophan reactions.

No. 2—not tested.

No. 3—strong tryptophan reaction.

No. 4—no tryptophan reaction.

*Seeds soaked in water for twenty-four hours.*—Seeds from the same lot used in the above experiment were soaked in distilled water for twenty-four hours, the hulls removed, and the cotyledons ground in a mortar and 1.5<sup>gm</sup> of the paste tested in the same way as the dry bean meal, and with the same results.

*Seeds soaked for forty-five hours.*—The beans not used in the last experiment were soaked twenty-one hours longer, peeled, and the tests repeated, with the same results.

*Seeds soaked twenty-four hours and germinated in sand three days.*—At this stage the hypocotyls were about one inch long. The cotyledons were removed, ground in a mortar, and the paste tested as in the previous experiments. The result was the same, the Witte peptone was attacked and the seed proteids were not.

*Seeds soaked twenty-four hours and germinated six days.*—The cotyledons from the young plants with hypocotyls two to three inches long were removed and ground to a paste. One gram of this was placed in each of six test tubes and other additions made as follows:

- No. 1—10<sup>cc</sup> H<sub>2</sub>O + toluol.
- No. 2—10<sup>cc</sup> H<sub>2</sub>O + toluol—boiled.
- No. 3—10<sup>cc</sup> H<sub>2</sub>O + 0.1 per cent. of citric acid + toluol.
- No. 4—10<sup>cc</sup> H<sub>2</sub>O + 0.1 per cent. of Na<sub>2</sub>CO<sub>3</sub> + toluol.
- No. 5—10<sup>cc</sup> H<sub>2</sub>O + 0.2<sup>gm</sup> Witte peptone + toluol.
- No. 6—10<sup>cc</sup> H<sub>2</sub>O + 0.2<sup>gm</sup> Witte peptone—boiled + toluol.

After nineteen hours in the incubator the contents of each tube were boiled, acidified, filtered, and the filtrates tested with these results:

- No. 1—no tryptophan nor biuret reactions, Millon's?
- No. 2—not tested.
- No. 3—no tryptophan reaction, biuret? Millon's?
- No. 4—no tryptophan reaction, biuret? Millon's?
- No. 5—strong tryptophan reaction.
- No. 6—no tryptophan reaction.

• *Seeds soaked twenty-four hours and germinated ten days in the dark.*—The cotyledons at this age of the plant were comminuted and tested in tubes as follows:

- No. 1—ground cotyledons + H<sub>2</sub>O + toluol.
- No. 2—ground cotyledons + H<sub>2</sub>O + toluol + uncoagulated egg albumen.
- No. 3—ground cotyledons + H<sub>2</sub>O + toluol + edestin.
- No. 4—ground cotyledons + H<sub>2</sub>O + toluol + Witte peptone.

After eighteen hours in the incubator the tests showed that only the Witte peptone had undergone proteolysis.

*Cotyledons of eleven-day old seedlings grown in light.*—Beans allowed to germinate in washed sand, with a good supply of light, for eleven days had attained a height of five to six inches and had two well developed leaves besides the shriveled cotyledons. The cotyledons were found still to contain an active ereptase.

*Cotyledons of etiolated seedlings thirteen days old.*—These cotyledons gave convincing evidence of the presence of ereptase, but no tryptase.

Besides testing the cotyledons of germinating beans by the method of autodigestion, extracts were also prepared with glycerin and 20 per cent. alcohol. The tests applied to these extracts showed that they were incapable of digesting the bean proteids or boiled fibrin.

It should be noted that OSBORNE and HARRIS<sup>17</sup> have found that phaseolin, the globulin which makes up the main proteid store of the resting bean, gives but a faint Adamkiewicz reaction. Therefore the absence of a tryptophan reaction in the autodigestion experiments with the bean cotyledons would not be conclusive evidence of the lack of proteolysis. The use of the Millon's reaction for tyrosin and the biuret reaction for albumoses and peptones would have shown the presence of the products of peptonization or proteolysis had they been present. Still more conclusive evidence that the enzyme in question does not act on the unaltered proteids of the cotyledons is afforded by the more thorough study of the enzyme.

Beans were allowed to germinate for four days and the cotyledons separated and ground in a mortar to a paste. Forty grams of this pulp were extracted with 200<sup>cc</sup> of water and 5<sup>cc</sup> of toluol. The extract was removed from the tissue residue by straining through fine muslin, and, since phaseolin is soluble in water and the salts of the seed, this milky looking fluid was rich in proteid matter. The 200<sup>cc</sup> of extract were divided between two flasks and one of the portions boiled. After digesting for seventeen and one-half hours, a comparative quantitative estimation of the amount of nitrogen in the proteid decomposition products was made in the following manner. Fifteen cubic centimeters of each digestion fluid were mixed in a dry beaker with 15<sup>cc</sup> of tannic acid reagent (7 per cent. of tannic acid dissolved in 2 per cent. acetic acid) and the precipitates removed by filtration. Nitrogen determinations were made in duplicate by the Kjeldahl method on 5<sup>cc</sup> of each filtrate. The amount of standard acid required to neutralize the ammonia formed by the sulphuric acid treatment was, in the unboiled digestion, 0.7<sup>cc</sup>; in the boiled digestion 0.5<sup>cc</sup>. The digestions were allowed to proceed for two

<sup>17</sup> OSBORNE and HARRIS, *loc. cit.*

days longer and the tests repeated. This time the unboiled digestion required 0.5<sup>cc</sup> of acid; the boiled digestion required 0.5<sup>cc</sup>.

This experiment was repeated, using different conditions of reaction to make sure that such conditions played no part in the results previously obtained. Fifty grams of cotyledons from seven-day etiolated bean seedlings were comminuted and an extract prepared as before. This was divided between five flasks as follows:

No. 1—50<sup>cc</sup> extract.

No. 2—50<sup>cc</sup> extract—boiled.

No. 3—50<sup>cc</sup> extract + 0.14<sup>gm</sup> citric acid ( $= \frac{N}{25}$  acid).

No. 4—50<sup>cc</sup> extract + 0.106<sup>gm</sup> Na<sub>2</sub>CO<sub>3</sub> ( $= \frac{N}{25}$  Na<sub>2</sub>CO<sub>3</sub>).

No. 5—50<sup>cc</sup> extract + 2<sup>gm</sup> Witte peptone.

Toluol was added in equal amount to all the flasks. The quantitative estimations were made in the same manner as in the last experiment except that 10<sup>cc</sup> of each filtrate were used for an analysis instead of 5<sup>cc</sup>. In place of a boiled control for no. 5, a determination was made at the start of the experiment, when it appeared that 1.4<sup>cc</sup> of standard acid were required to neutralize the ammonia formed from the nitrogen compounds in 10<sup>cc</sup> of the filtrate from the tannic acid precipitate. After three days' digestion quantitative determinations were made on all.

No. 1—required 1.3<sup>cc</sup> of standard acid.

No. 2—required 1.0<sup>cc</sup> of standard acid.

No. 3—required 1.5<sup>cc</sup> of standard acid.

No. 4—

No. 5—} analyses lost by breaking of the apparatus.

Three days later the tests were repeated.

No. 1—required 1.4<sup>cc</sup> standard acid.

No. 2—analyzed 5<sup>cc</sup> of digestion fluid = to 10<sup>cc</sup> of tannic acid filtrate; required 4.3<sup>cc</sup> standard acid.

No. 3—required 1.4<sup>cc</sup> standard acid.

No. 4—required 1.1<sup>cc</sup> standard acid.

No. 5—required 6.5<sup>cc</sup> standard acid.

The digestion fluid of no. 5 at the close of the experiment gave a strong tryptophan reaction. The variations among the digestions, except no. 5, are within 0.5<sup>cc</sup> of standard acid; in such a method

these differences cannot be held to show the presence of a trypsin-like enzyme, especially when we see the change in the digestion containing Witte peptone which at first required  $1.4^{\circ}\text{C}$  of acid for  $10^{\circ}\text{C}$  of filtrate and at the close  $6.5^{\circ}\text{C}$ .

Being convinced by the experiments tried that the resting and germinating bean contained an ereptase, I attempted to separate it from the mass of other materials in the seed extracts.

One hundred and fifty grams of bean meal were extracted for five hours with  $375^{\circ}\text{C}$  of water with the addition of toluol and chloroform. The fluid was strained and pressed out through cheese cloth, the residue mixed with  $150^{\circ}\text{C}$  of water and this likewise removed. The total extract, amounting to  $450^{\circ}\text{C}$ , was allowed to settle over night to get rid of the starch, etc. by sedimentation. The next morning the supernatant fluid was siphoned off and filtered three times through pulp filters, yielding  $365^{\circ}\text{C}$  of an opalescent fluid. This was half saturated with ammonium sulphate by adding an equal volume of saturated ammonium sulphate solution. The flocculent precipitate *A* was removed by filtration, and to the filtrate saturated ammonium sulphate solution was added to make two-thirds saturation. Precipitate *B* was likewise removed and ammonium sulphate added to three-quarters saturation. With this concentration of the salt nothing but a turbidity resulted; accordingly ammonium sulphate in substance was added to saturation, yielding the precipitate *C*. A small portion of each precipitate was placed in a test tube and mixed with Witte peptone and water; after standing over night in the incubator the fluids were tested for tryptophan. The results showed that *A* contained sufficient ereptase to cause a strong tryptophan reaction, *B* a weak one, and *C* none at all. Each precipitate was dissolved in water so far as possible, and the turbid solution placed in dialyzing bags and dialyzed until practically free from sulphates. In *A* a considerable amount of phaseolin was precipitated on the sides of the dialysis; this was filtered off, washed with water, and both the clear filtrate and the globulin tested with Witte peptone. It was found that the ereptase had remained in solution and had not been carried down with the precipitated proteid. The solutions of the precipitates *B* and *C*, after dialysis, were found to have respectively a weak action on Witte peptone and no action at all.

The ereptase solution obtained from *A* gave a weak biuret reaction and a faint coagulum on heating. Attempts to precipitate the enzyme by means of uranium acetate according to Jacoby's method failed; no precipitate was obtained except in acid solutions in which the enzyme was destroyed. The ereptase was tested with crystallized edestin from hemp seed, crystallized excelsin from the Brazil nut, phaseolin from the bean, boiled fibrin, and Witte peptone. The native proteids were all unattacked and the Witte peptone was actively digested.

An ereptase solution was prepared from 1500<sup>gm</sup> of bean meal by extraction with water, filtering the extract, half saturating the solution with ammonium sulphate, and dialyzing the solution obtained from this half saturation precipitate. A perfectly clear solution resulted after filtering off the phaseolin precipitated by dialysis, and this was dried at 40 to 50° C., yielding 2.9<sup>gm</sup> of a golden yellow powder. This powder was found to be active in digesting Witte peptone, although it seemed that the purification and drying had considerably diminished the power of the enzyme. This protease preparation was tested with some of the fractions of Witte peptone which had been separated by Pick's<sup>18</sup> method and with a preparation of phaseolin. The first experiment was carried out using the secondary protease preparations without the removal of the ammonium sulphate left adherent by the method of separation.

One and one-half grams of the enzyme preparation mentioned above were dissolved as completely as possible in 300<sup>cc</sup> of water, 35<sup>cc</sup> of this solution measured into each of five flasks, and 2<sup>cc</sup> of toluol added. Proteids were added as follows:

- No. 1—1<sup>gm</sup> of phaseolin.
- No. 2—1<sup>gm</sup> of proto-protease.
- No. 3—1<sup>gm</sup> of hetero-protease.
- No. 4—1<sup>gm</sup> of secondary albumose *A*.
- No. 5—1<sup>gm</sup> of secondary albumose *B*.

After shaking, 15<sup>cc</sup> were removed from each flask, 15<sup>cc</sup> of tannic acid reagent added, and the precipitates filtered off. Analyses of 10<sup>cc</sup> of each filtrate were made in duplicate:

- No. 1—required 0.7<sup>cc</sup> of standard acid.
- No. 2—required 0.6<sup>cc</sup> of standard acid.

<sup>18</sup> PICK, Zeitschr. Physiol.-Chem. 24:246. 1898.

No. 3—required 0.8<sup>cc</sup> of standard acid.

No. 4—required 10.3<sup>cc</sup> of standard acid.

No. 5—required 7.6<sup>cc</sup> of standard acid.<sup>19</sup>

After six days in the incubator the quantitative estimations were repeated.

No. 1—required 0.6<sup>cc</sup> standard acid = gain of 0.0<sup>cc</sup>.

No. 2—required 1.9<sup>cc</sup> standard acid = gain of 1.3<sup>cc</sup>.

No. 3—required 1.3<sup>cc</sup> standard acid = gain of 0.5<sup>cc</sup>.

No. 4—required 10.9<sup>cc</sup> standard acid = gain of 0.6<sup>cc</sup>.

No. 5—required 9.2<sup>cc</sup> standard acid = gain of 1.6<sup>cc</sup>.

The results in the case of the phaseolin, the proto-proteose, and the deutero-albumose *B* are well defined; those with the hetero-albumose and the deutero-albumose *A* were not sufficiently marked to lead to a definite conclusion.

A second experiment was tried with the four proteose preparations after the ammonium sulphate had been removed from the two deutero-proteoses. In these trials, instead of using the ereptase preparation used in the previous experiment, an extract was made from some bean meal and filtered several times through pulp filters until it was nearly clear. Of each of the four proteoses 0.125<sup>gm</sup> was dissolved in 25<sup>cc</sup> of water. Ten cubic centimeters of the bean extract were placed in each of eight test tubes and four of the portions boiled. Ten cubic centimeters of each proteose solution were added to a boiled, and 10<sup>cc</sup> to an unboiled, portion of the extract. Nine drops of toluol were added to each tube, the tubes corked, shaken, and kept in the incubator for sixty-five hours. At the expiration of that time the contents of all the test tubes were boiled and filtered. Of each filtrate 10<sup>cc</sup> were removed to a clean test tube, 5<sup>cc</sup> of a 10 per cent. sodium hydroxide solution added, and then dilute copper sulphate to the maximum biuret reaction. After standing for several minutes the strengths of the biuret reactions from the boiled and unboiled digestions of the different proteoses were compared. The reactions showed that all of the proteoses were attacked by the enzyme. The portions of the filtrates not used in the comparative biuret reactions were employed to test for tryptophan. The unboiled digestions with proto-proteose, hetero-proteose, and deutero-proteose *A* gave

<sup>19</sup> The ammonium sulphate in the last two proteose preparations accounts for the high nitrogen in the filtrates from the tannic acid precipitates.



distinct tryptophan tests, that with deuterio-proteose *B* was very faint; none of the boiled digestions showed any trace of tryptophan.

In summing up the results of the experiments described above, we may note that evidence of the presence of a protease has been obtained in the leaves of the spinach and cabbage, the blossoming heads of *Daucus Carota* and the developing seeds of that plant, in the leaves and unripe seeds of the chestnut, the etiolated seedlings of *Phaseolus Mungo*, the seeds and seedlings of *Cucurbita maxima*, and the seeds of *Cucurbita Pepo*. In the case of *Phaseolus vulgaris*, experiments with all stages of the germination of the seed have shown that the cotyledons always contain an enzyme of the erepsin group, and at no time can any evidence of the presence of an enzyme capable of attacking the proteids of the seed be obtained. This ereptase may be removed from the bean extracts by half saturation of the solution with ammonium sulphate. On dissolving this precipitate in water and dialyzing the solution free from sulphates, the enzyme is obtained in a solution which is perfectly clear and gives but feeble reactions for proteids. A preparation of the enzyme may be obtained by drying this solution at a temperature below 50° C. The enzyme acts on the proto-proteose, the hetero-proteose, and the deuterio-proteoses, separated from Witte peptone; it is quite inactive on phaseolin of the bean, excelsin of the Brazil nut, edestin of the hemp seed, and boiled fibrin.

There can be no doubt but that the large proteid store in bean seeds is utilized in germination, and in all probability this utilization is preceded by cleavage to the amido-acids, hexon bases, etc. What effects this cleavage, and what part, if any, the ereptase plays, are unsolved problems. It is likewise unknown whether or not this enzyme occurs in other parts of the plant or whether enzymes of the trypsin type are present in certain tissues.

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## DEVELOPMENT OF SPORANGIUM IN BOTRYCHIUM.

CONTRIBUTIONS FROM THE HULL BOTANICAL  
LABORATORY. LXXI.

IRA D. CARDIFF

(WITH PLATE IX)

THE present work upon Botrychium was taken up with the purpose of investigating what was thought by some to be septation caused by sterilization of mother-cells in the sporangium of *B. ternatum*. Both *B. ternatum* and *B. virginianum* were examined, and the two species were found to be essentially the same in their sporangial development. The material of *B. virginianum* was collected near Woodville, Indiana, March 14, 1904; that of *B. ternatum* was collected near Sullivan, Ohio.

The early stages in the development of the Botrychium sporangium were studied by BOWER (1), CAMPBELL (2), and GOEBEL (5), but apparently none of them studied the interesting later stages. In the present work, though a number of preparations were examined, no special attention was given to the early development further than to confirm the studies of the above mentioned investigators, namely, that the sporogenous mass originates from a single hypodermal archesporial cell. CAMPBELL (2) says that the later divisions in the archesporium do not follow any definite rule, but take place irregularly. This does not accord with my observations, the divisions in *B. ternatum* and *B. virginianum* taking place with great regularity. CAMPBELL implies that his fig. 129, C, which shows no regularity in cell-arrangement, is in the mother-cell stage. If this is true, it indicates an unusually small output for a Botrychium. HOLTZMAN (6) made some observations upon the later development of the sporangium of Botrychium, but BOWER (1) thinks that the sequence of segmentations, as shown in HOLTZMAN's figs. 3-6, is not sufficiently intelligible, and should be investigated afresh. He thinks that HOLTZMAN's description suggests a mode of segmentation more clearly analogous to that in leptosporangiate ferns.

In the sporangium of *Lycopodium*, the sporogenous mass is divided into blocks of cells, each block apparently being the descendant of a single archesporial cell. The blocking here is evidently related to a multicellular archesporium. In the *Botrychium* sporangium there occurs a blocking of the sporogenous mass that must have a different cause, as the archesporium is unicellular. The single hypodermal archesporial cell divides usually anticleinally, then pericleinally (*fig. 1*). Regular divisions then follow, as shown by *fig. 2*. At the stage shown in *fig. 2* the wall is six to eight cells in thickness, including the tapetum; and the extremely glandular character of the two inner layers of cells indicates that they are definitely set apart as tapetum. In the tapetum at this stage walls are formed both pericleinally and anticleinally. The divisions in the sporogenous mass occur with remarkable regularity. The position of the original walls, from stages shown in *figs. 1* and *2*, are still perfectly apparent up to the spore mother-cell stage (*fig. 3*). At this stage the sporogenous mass has somewhat the appearance of the spermatogenous mass in a bryophytic antheridium, except for the size of the cells and the character of the nuclei. By the time the mother-cell stage is reached, the tapetum has become four or five cells thick, is quite glandular in appearance, and there is no further evidence of mitotic division. The sporangium wall-cells adjacent to the tapetum have commenced to collapse as a result of the drain upon them by the tapetum.

Probably the most common and most primitive method of nourishment of mother-cells is by abortion and absorption of a portion of the mother-cells to form a diffuse tapetum, as in *Equisetum*. Another method is by the formation of sterilized tracts from potentially sporogenous tissue through which material may be conducted to the interior of the sporangium, as the trabeculae of *Isoetes* or the septations in the microsporangia of *Lemna minor*.

In the sporangium of *Botrychium*, no sterilization of either kind was found, every mother-cell functioning. So far as I was able to determine, division up to the mother-cell stage is simultaneous throughout the sporogenous mass, yet the original blocks (*fig. 3*) of sporogenous cells still remain perfectly distinct. As the mother-cell enters upon the synapsis stage, the original walls or wall separating

the blocks is apparently thicker, and by the time the spirem is formed the blocks have begun to separate. This separation takes place in the order in which the original walls were laid down in the archesporium and young sporogenous mass (*figs. 3, 4, 6, 7*). At about prophase the mass has separated into at least sixteen (in section) distinct and separated masses (*fig. 6*). "About" prophase is used, since with the separation of the blocks differences in stages of division begin to appear, so that the cells throughout the entire sporogenous mass are not in the same stage, though those in the same block are always in the same stage.

The progressive separation into smaller blocks continues in the same manner in which the first blocks were formed. It takes place along the same lines and in the same order in which the earlier walls were laid down. Whatever stimulus caused the simultaneity of division during the early life of the sporangium seems to have been interfered with here by the cleavage into disjoined blocks, for in the same sporangium the blocks are in different stages of division, it being quite common to find four or five stages. For example, in three adjacent blocks, the cells of one were in early metaphase, of another in telophase, and of the third in anaphase. In another case blocks were found in the same sporangium varying from metaphase of first to metaphase of second division; and it is very common to find them varying from metaphase of first to prophase of second division. One sporangium was found in which all the cells of one-half the entire sporogenous mass were in metaphase, while those of the other half were in telophase. All of the sporogenous tissue throughout its entire development appears in a vigorous and perfectly normal condition.

What may be the cause of this retention of their individuality by the developing sporogenous cells is difficult to say. In regard to bryophytic antheridia this phenomenon has been explained as due to the independent development of the original spermatogenous cells; and there is no further blocking of the spermatogenous mass after the periclinal walls which cut off this mass from the antheridial wall layer have been formed. The difference in rate of development of these blocks has been attributed to differences in food supply, or to some purely physiological cause. It seems that as much might be

said of the blocking in a *Botrychium* sporangium; though each division, from the very first almost to the formation of the mother-cell, separates masses which retain their individuality throughout their further development. The rate of growth, however, and apparently the food supply are absolutely the same for all the blocks up to the mother-cell stage. It would seem that in such large sporangia some blocks or cells would be more favorably located than others with reference to food supply or conditions of growth, and there would be greater growth on the part of some regions than others, thus causing irregularities in the arrangement of cells, such as is found in most sporangia, instead of the very regular arrangement in those of *Botrychium*. Therefore, the above mentioned physiological explanation in regard to bryophytic antheridia is not entirely satisfactory.

What may be the exact cause of this progressive separation of the sporogenous mass along lines where the earlier walls were laid down is impossible at present to say. To me, the most reasonable explanation which can be offered is that the middle lamellae of the walls are acted upon by an enzyme at a time when the sporogenous mass is greatly in need of food. As the lamellae grow older their composition may change, so that they are more easily digested than those more recently formed, thus effecting a progressive separation of the sporogenous tissue. As the blocks become separated, and wholly or partially surrounded by the tapetum, some blocks will of necessity be under slightly different conditions of osmotic pressure or chemical stimulation than others, thus bringing about differences in the rate of their development.

In *Botrychium* the tapetum is derived from the wall, and absolutely no contribution is made to it from the sporogenous tissue. By the time the sporogenous mass has reached as much as sixty-four cells, the tapetum is clearly delimited from the sporangial wall and is two cells in thickness. From this time on periclinal divisions take place rapidly until the spore mother-cell stage is reached, when the tapetum is four or five cells in thickness and very glandular in appearance. At the first separation of the blocks (*figs. 3 and 4*) in the sporogenous mass—about the synapsis stage—the cell walls of the inner layer of tapetal cells begin to disintegrate. Some of these inner cells are at this time binucleate, while the nuclei of the next one or two layers

of cells are in process of division amitotically, and can be found in all stages. All the tapetal nuclei have now increased much in size, those of the young tapetal cells being  $8\mu$  in diameter, and those of the later stage 15 to  $20\mu$ . As the blocks of sporogenous cells continue to be formed and more widely separated, the tapetum commences to grow rapidly. The number of nuclei increases greatly, as well as the volume of the cytoplasmic mass in which they float. This pushes inward between the blocks with quite a regular outline (*fig. 6*). At prophase of the first division of the mother-cell, a section of the sporangium shows that these tapetal plates have extended almost across the sporogenous mass between the first formed blocks, and have commenced to grow inward between the blocks of later formation (*fig. 6*). This rapid tapetal growth continues pushing thinner and thinner plates between the smaller blocks as they are formed (*figs. 7, 8, 9*), making a network which finally invests the individual tetrads, or groups of two or four tetrads (*fig. 9*); and at last the spores separate and float in this tapetal mass. The original thicker plates of tapetum may often be found after the spores are completely formed.

As this excessive tapetal growth takes place, the cell walls of the original tapetum break down successively from the inner layers outward, until at metaphase of the mother-cell the walls of only the outermost layer of tapetal cells remain. By the time anaphase of second division (*fig. 8*) is reached, the last walls of the tapetal cells have entirely disappeared, and the inner cells of the sporangial wall begin to take on tapetal characters; especially is this true of the nuclei which resemble tapetal nuclei very closely (*fig. 9*). The cell walls, while they collapse, have not been found to disintegrate entirely, as in the case of the true tapetum. In fact, there is no reason why these inner layers of sporangial wall might not be called tapetum.

Probably the most interesting feature of the development of the Botrychium sporangium is the unusual growth of the tapetum. As before mentioned, it increases greatly in volume and in number of nuclei, yet not a wall is formed anywhere, though it was stained especially for walls. The nuclei are found in all stages of amitotic division (*figs. 5, 8, 9*), but no evidence of mitosis is found. They take stains strongly, are exceedingly large, as mentioned above, and have an unusually thick nuclear membrane. That the nucleus

bears an important relation to the metabolic processes of the cell is too well recognized to need discussion, and this enlargement of nuclei, or increase in nuclear surface, is undoubtedly in response to the increased demand for nourishment on the part of the sporogenous tissue at this stage.

It has been noted frequently that the ovarian follicle cells of arthropods have many large nuclei which divide amitotically, and this has been explained by FLEMMING (4) and CHUN (3) as being a means of securing more rapid metabolic processes between cytoplasm and nucleus through the use of a larger nuclear surface. Our reliable knowledge of the process of amitosis is so meager that one can at this time venture only a tentative explanation of the nuclear behavior in the Botrychium tapetum. Whether amitosis can take place more rapidly than mitosis is unknown, but from the mechanics of the two processes, it would seem that the former would be much the more rapid. WILSON (9) considers that all nuclear division is the response to particular stimuli, and is probably incited by local chemical changes, an idea which is confirmed by PFEFFER (8) and NATHAN-SOHN (7), who were able to produce mitosis or amitosis at will in *Spirogyra orbicularis*. May we not then look upon amitosis in the tapetum as simply an acquired character due to the unusual demand upon it by the fertile tissue for nourishment at a particular period in its development? Walls being unnecessary, the energy of the organism would not be used in forming them.

As the spores commence to separate in the tetrad, the tapetal cytoplasm has entirely filled the sporangium and many of the nuclei have begun to disorganize, though they seem unusually persistent and many are found after the tetrad is fully formed. Later, when the spores are entirely separated and mature, the tapetum disappears.

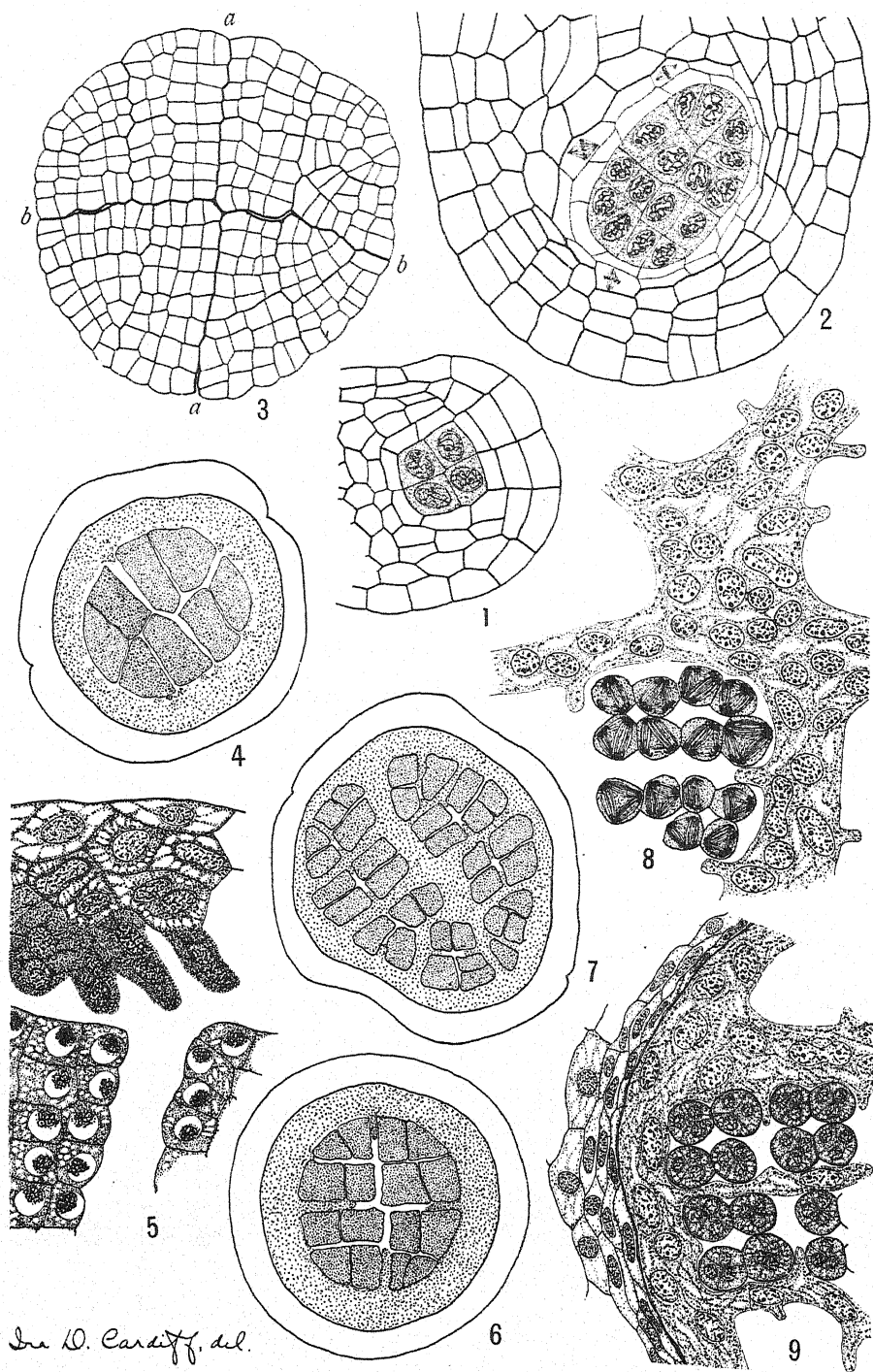
Thus we have here worked out the problem of nourishment in a large sporangium by a method entirely different from the two formerly mentioned, namely by the preservation of the individuality of sporogenous cells, thus enabling the mother-cell mass to separate easily into regular blocks, and leaving straight open passageways through which a non-sporogenous tapetum grows rapidly, furnishing the required nourishment for the developing spores. As a general rule there are more spores provided for in a sporangium than nutri-

tive conditions will allow, and there are usually two methods by which this difficulty is overcome: by abortion of mother-cells, and by arrangement for a succession of sporangia according to nutritive supply. In *Botrychium*, however, there is no abortion of mother-cells and very little difference in the stages of development of the different sporangia in a spike. The nutritive supply is equal to the demand of all mother-cells, probably owing, in part, to the slow growth of the plant, and also to the large amount of food material stored in the stem.

#### SUMMARY.

1. The sporogenous tissue develops from a single hypodermal archesporial cell.
2. As the successive sporogenous cells are formed, each retains its individuality throughout the development of the sporogenous tissue.
3. Divisions in the sporogenous tissue are simultaneous up to the mother-cell stage.
4. Beginning with the mother-cell stage, the sporogenous mass separates successively into blocks of cells in the same order in which the earlier cells were formed.
5. The blocks develop independently, and at a different rate in the same sporangium, though all cells of one block develop at the same rate. Whatever stimulus caused the simultaneity of division in early sporogenous tissue, is interfered with by separation of the cells into disjoined groups.
6. The progressive separation of the sporogenous mass is probably caused by the digestion of the middle lamellae.
7. All mother-cells produce spores.
8. The tapetum is of non-sporogenous origin.
9. With the separation of mother-cell groups, the tapetum grows rapidly between them without the formation of walls; the nuclei increasing greatly in size, and dividing amitotically.
10. The problem of nourishment in large sporangia may thus be solved by individual development of sporogenous cells, by their later separation into regular groups, and the rapid growth of tapetum between them.
11. The nuclei of the old tapetum are four times the size of those in younger stages of its development.





Dr. D. Cardiff, del.



12. Amitotic division and increase in size of nuclei are both devices for rapidly increasing nuclear surface, thus effecting a larger increase of metabolic products.

I am indebted to Professor JOHN M. COULTER and Dr. CHARLES J. CHAMBERLAIN for criticism and advice.

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#### EXPLANATION OF PLATE IX

All figures were made with Zeiss objectives and oculars and Bausch Lomb camera lucida. The original drawings were reduced one-half in reproduction.

FIG. 1. Young sporangium.  $\times 900$ .

FIG. 2. Sporogenous tissue of thirty-two cells; tapetum two cells thick and divisions taking place both periclinally and anticlinally.  $\times 900$ .

FIG. 3. Sporogenous tissue in mother-cell stage showing regularity in cell arrangement; the two original walls, *a* and *b*, beginning to separate.  $\times 400$ .

FIG. 4. Sporangium showing sporogenous tissue separating into blocks along the original walls.  $\times 150$ .

FIG. 5. Portion of fig. 4; mother-cells in synapsis; commencement of tapetal growth.  $\times 900$ .

FIG. 6. Sporangium showing sporogenous tissue separating along original walls shown in fig. 2; plates of tapetum extending between earlier formed blocks.  $\times 150$ .

FIG. 7. Sporangium showing sporogenous tissue separated into blocks in each of which the cell division is simultaneous.  $\times 150$ .

FIG. 8. Portion of sporangium showing separation of the forming tetrads, also the large increase in the number of tapetal nuclei.  $\times 900$ .

FIG. 9. Later stage than shown in fig. 8.  $\times 900$ .

PHYSIOLOGICAL PROPERTIES OF BOG WATER.  
CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY.  
LXXII.

BURTON EDWARD LIVINGSTON.

(WITH THREE FIGURES)

ALTHOUGH it has been shown (1) that water from the bogs of the northern United States contains solutes to such a very small amount that its osmotic pressure is generally not appreciably above that of the river swamps and lakes of the same region, still the generally observed xerophilous character of bog vegetation may be due to small amounts of dissolved substances of such nature that they affect the plants chemically through toxic stimulation. Having found that metallic ions affect the vegetative growth of the polymorphic *Stigeoclonium* with which the author has been experimenting for some time (2), and that the effect thus produced is identical with the response of the alga to high osmotic pressures, it was suggested that this alga might be used as an indicator in a study of the physiological properties of bog waters. In accordance with this suggestion, natural waters of a number of different types were collected in bottles, filtered through filter paper, and tested as culture media for the alga. The result of these tests is, briefly, that many bog waters act upon the plant like poisoned solutions. Details of the work are given in the following pages.

The form of *Stigeoclonium* here used has already been shown (2-6) to take either of two forms according to the medium in which it is grown. In solutions of low osmotic pressure at ordinary temperatures it assumes the form of branching filaments composed of cylindrical cells. In the same solutions at a temperature slightly above the freezing point of water, and at ordinary temperatures in solutions similar to these but poisoned with certain metallic salts, as well as at ordinary temperatures in solutions of high osmotic pressure, the plant takes the palmella form, in which the cells are spherical or nearly so and lie in the medium singly or in irregular groups. If

filaments are taken from the conditions which favor their growth and are placed in those favoring the palmella form, their cells round off and partially or completely separate, they begin to divide slowly in all planes, and the result is the typical form for these conditions. A return to the conditions for filaments is followed by the resumption of that form, partly by the growth of filaments directly from the palmella masses, and partly by the production of zoospores which germinate to form new filaments. Zoospores are not produced in solutions of high pressure, and they fail to germinate in solutions which produce the palmella form, though they are produced in the cold and in poisoned solutions.

The waters tested in these experiments are in large part the same as were used in the determination of the osmotic pressure (1). The work was carried on partly at the New York Botanical Garden and partly at the University of Chicago, and extended from June 1902 to January 1905. The cultures were made in the manner described for water cultures of this plant in the author's earlier papers.

Since a number of authors have loosely attributed SCHIMPER's "physiological dryness" (7) of bogs to acidity, titrations of most of the natural waters here employed were made with  $n/100$  KOH solution, using phenolphthalein as indicator.<sup>1</sup>

Data from the experiments are given in the following table. In the column of responses, F—F denotes that the filamentous form persisted as such when placed in this particular water. F—P denotes that the original filaments became palmella and that no new filaments were produced. F— $\frac{1}{2}$ P denotes that filaments persisted, but that there was also a marked production of palmella. A number of cultures were made with each of the waters, and the result is the general one for all. The cultures were continued for two to four weeks. The acidity data are given in terms of normal acid and the pressure in terms of millimeters of mercury at 25°C.

From the table it is seen at once that in some of the waters the palmella form was produced; in others it was produced in some measure, but filaments persisted; and in still others the filamentous

<sup>1</sup> Of the indicators at hand this was the best, although it is assuredly not perfect for such acids as are probably present in these waters.

## DATA FROM THE EXPERIMENTS

Source of water and nature of vegetation	Response of Steigeoclonium	Osmotic pressure of water, mm. of Hg	Acidity of water in terms of normal acid
Drained swamps of Hackensack River, N. J. (river swamps)—			
Average of six samples.....	F— $\frac{1}{2}$ P	50	0.00192
Maximum of six samples.....	.....	..	0.0042
Minimum of six samples.....	.....	..	0.001
New York City supply, Croton and Bronx Rivers.....	F—F	50	0.0005
Chicago City supply, Lake Michigan.....	F—F	100	Always alkaline, about 0.0015
Grand River, Grand Rapids, Mich.....	(see fig. 1) F—F	100	As last, or more alkaline
Aetna, Ind. ( <i>Rhus vernix</i> , <i>Drosera</i> )—			
Average of three samples pressed from black peat.....	F— $\frac{1}{2}$ P	100	.....
Miller, Ind. ( <i>Larix</i> , <i>Rhus vernix</i> )—			
Average of two samples pressed from black peat.....	F— $\frac{1}{2}$ P	50	0.0003
Oconomowoc, Wis.* (typical <i>Larix</i> swamp), ditch.....	F—P	200	0.0004
Stewart Ridge, Ill., average of three samples pressed from black peat.....	F—F	150	0.0002
Ann Arbor, Mich.†			
First Sister Lake bog ( <i>Larix</i> , <i>Chamaedaphne</i> , <i>Sphagnum</i> )—			
Sample A.....	F—P	50	0.0033
Sample B.....	(see fig. 2) F—P	440	0.0038
West Lake bog ( <i>Sphagnum</i> , <i>Chamaedaphne</i> , <i>Potentilla palustris</i> , <i>Salix</i> )—			
Sample A.....	F—P	100	0.0026
Sample B.....	F—P	150	0.0024
Tom's River, N. J. ( <i>Chamaecyparis</i> , <i>Sphagnum</i> , <i>Chamaedaphne</i> , <i>Sarracenia</i> , <i>Oxycoccus</i> )—			
Sample A, pressed from <i>Sphagnum</i> .....	F—F	170	0.0004
Sample B, beneath <i>Sphagnum</i> .....	F—P	140	0.00048
Sample C, pressed from black peat.....	F—P	90	0.0003
Sample D, margin of pond.....	F—P	40	0.0003
Sample E, ditch.....	F—P	50	0.0003
Richmond, Staten Island, N. Y. ( <i>Alnus</i> , <i>Eriophorum</i> , <i>Sphagnum</i> )			
Sample A, edge of pond.....	F—P	90	0.0015
Sample B, decayed leaves.....	F— $\frac{1}{2}$ P	110	0.0022
Sample C, ditch.....	F—F	90	0.0008
Sample D, pressed from <i>Sphagnum</i> .....	F—F	100	0.001

\* This water was obtained for me by Dr. H. C. COWLES of this laboratory.

† The samples from Ann Arbor were obtained for me by Dr. H. N. TRANSEAU, of Alma College, Mich.

form persisted without the production of palmella at all. The characteristic forms of this plant in three different waters are shown in figs. 1, 2, and 3, which are to be compared with previously published figures, and are self-explanatory.

As has been shown in the case of many inorganic poisons (5), the production of the palmella form is sometimes accompanied in these waters by a stimulation of zoospore production. Usually, however, the swamp water acts more like low temperatures, producing the vegetative response without either accelerating or retarding the reproductive activity.

The palmella response in certain of these waters may be due,

*a priori*, to either of two sets of factors, the osmotic pressure of the solution or the chemical nature of the solutes. Since the experiments were carried on at room temperature, it is unnecessary to consider low temperature as a possible stimulus.

In the work on the influence of osmotic pressure upon this plant it was found (2, 3) that there is no tendency to form palmella till a pressure of about 1618.6<sup>mm</sup> of mercury has been attained. Filaments still persist at a pressure of 3237.1<sup>mm</sup>, but have practically all disappeared at a pressure of 6474.2<sup>mm</sup>. But no swamp water studied has a pressure at all approaching the lower limit for even the incipient

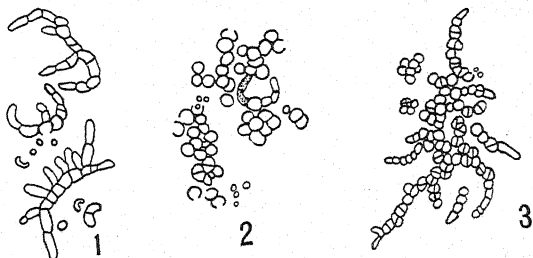


FIG. 1. Stigeoclonium filaments in Lake Michigan water.

FIG. 2. Stigeoclonium, palmella form from filaments, in water from West Lake, Ann Arbor, Michigan, sample A.

FIG. 3. As fig. 2, but in water from First Sister Lake, Ann Arbor, sample B.

formation of palmella. Therefore, we are forced to the conclusion that the palmella response in these bog waters is due to the chemical nature of the solutes. The plant grows well as filaments for a long time in distilled water, so that it is impossible to relate the reasons to absence of inorganic salts.

Definite knowledge of the chemistry of bog water is beyond our reach at present. It appears that all bogs are acid to some degree, and there has been a tendency for many authors, *e. g.*, SCHIMPER (7, pp. 4, 8, 657, etc.), to attribute the peculiarities of bog plants to this property. In the author's study of chemical stimulation (5) it was found that nitric and sulfuric acids produce palmella at concentrations of from 0.0001*n* to 0.0006*n*. The natural swamp waters are uniformly more acid than this; therefore, were the acid property of the latter due to either of these mineral acids, we should expect *all* of these waters to produce the palmella response. This is obviously

not the case, and so it seems highly probable at least that the stimulating factor of bog waters is not the hydrogen ion.

Further, a comparison of the acidity figures with the response of the plant in the different waters shows clearly that the former data could not be used as a criterion for the prediction of the latter. This is clearly brought out in the following list, in which the acidity figures are arranged in order of their magnitude, with the responses occurring in the corresponding water placed after each. Alkalinity 0.0015*n*, F; acidity 0.0002*n*, F; 0.0003*n*, F,  $\frac{1}{2}$ P, P; 0.0004*n*, F, P; 0.00048*n*, P; 0.0005*n*, F; 0.0008*n*, F; 0.001*n*, F; 0.0015*n*, P; 0.0019*n*,  $\frac{1}{2}$ P; 0.0022*n*,  $\frac{1}{2}$ P, P; 0.0026*n*, P; 0.0033*n*, P; 0.0038*n*, P. The lower acidities appear to produce both filaments and palmella, the higher ones only palmella. This would seem to indicate that, while high acidity is always accompanied by the presence of the stimulating substances, these substances are not necessarily accompanied by high acidity.

Boiling the stimulating waters for five or ten minutes and then rediluting to the original volume with redistilled water decreases their acidity from 30 to 50 per cent., but appears not to alter their stimulating power. Apparently the active substances are not volatile at 100° C. Diluting the Ann Arbor samples, and also those from Tom's River numbered 2, 3, and 4, with distilled water or with weak nutrient solution, decreases the toxic effect, and this effect practically disappears when the water has been diluted to twice its volume. This is evidence that the stimulating substances are present in extremely small amount.

The relation of the source of these waters and the type of vegetation growing therein to the physiological properties exhibited toward *Stigeoclonium* throws some light on the general problem of the xerophilous character of bog plants. The drained swamps of the Hackensack valley are not in any sense bogs. In many places, however, are found spots where *Sphagnum* has taken a foothold in small pools. *Eriophorum*, *Typha*, and some other semi-xerophilous plants are also found here. The water samples studied were taken from such places, and the experiments show that they possess the toxic property to a considerable degree. The data for this broad area of swamps are averaged from a large number of samples taken near Englewood and Closter, N. J., as well as from the western slope



above the palisades of the Hudson, where the water is held in the irregular rock basins.

The New York City water, although quite acid, is not active upon the alga. This water is from streams with well-drained river swamp margins. Lake Michigan water and the water of Grand River appear to be identical. Both are somewhat alkaline; neither has any physiological effect upon *Stigeoclonium*.

The Aetna and Miller swamps are practically alike; both are composed of black peat with no *Sphagnum*. The general nature of these swamps suggests an intermediate condition between bog and river swamp, leaning toward the former, and the water shows a marked tendency to produce *palmella*.

The bog near Oconomowoc has *Larix*, *Sphagnum*, *Vaccinium corymbosum*, *Oxycoccus*, *Chamaedaphne*, *Sarracenia*, etc. Its water has a very marked action upon the alga.

The Stewart Ridge swamp is a peat deposit but not a true bog. A few patches of *Sphagnum* seem to show a tendency in this direction, but the samples tested showed no effect upon the indicator plant.

The swamps of Ann Arbor are as typical and characteristic bogs as the author has seen. The character of their vegetation, consisting of *Larix*, *Drosera*, *Sarracenia*, *Andromeda*, *Chamaedaphne*, *Arethusa*, *Calopogon*, etc., agrees well with the fact that the water is markedly toxic toward the alga.

The vegetation upon all the vast stretches of lowland about Tom's River is practically alike; these are dense *Chamaecyparis* swamps, abounding in *Oxycoccus*, *Sphagnum*, *Sarracenia*, *Chamaedaphne*, etc. All the samples from here, with the exception of one pressed from living moss, produced the *palmella* response. It appears that the active bodies are more plentiful in the mass of dead material beneath the *Sphagnum* than in the moss itself.

The Richmond swamp is not a true bog, and yet it contains considerable amounts of loosely-growing *Sphagnum*, together with *Eriophorum*, *Typha*, etc. Here there appears a disagreement between the physiological properties of water samples from different parts. That from the ditch should be the most dilute, and shows no action upon the indicator. That from moss is again harmless; while that pressed from decayed leaves near by shows a marked toxic effect. The pond sample was taken up within a centimeter or two of sub-

merged powdery peat, and should be saturated or nearly so with any slightly soluble substances contained therein. Its active property is very marked.

From the last eight paragraphs it seems clear that the stimulating substances with which we have been dealing are present in swamp waters to an extent roughly proportional to the xerophilous character exhibited by the swamp vegetation. It is possible that the factor in such bogs which prevents the growth of plants other than xerophilous ones may be these unknown toxic bodies. They act upon *Stigeoclonium* in much the same manner as do drying media. Perhaps ordinary plants are affected by these substances with the same end result as though they were in a truly dry soil. If this be true it becomes easy to see how plants whose protoplasm is naturally adapted to dry situations may alone be able to thrive in these bogs.

The behavior of this alga toward dryness, cold, and bog water are quite parallel with results obtained by TRANSEAU (8) with *Rumex acetosella*. This author found that in dry mineral soil, *Rumex* produces thickened leaves reduced in size and with revolute margins, while the palisade tissue is very much increased in amount, and the epidermal cells are reduced in size and have thick, cuticularized outer walls. These changes give the plant, which in moist conditions is anything but a xerophyte, a very characteristic xerophilous structure. The same responses are exhibited, to a somewhat less degree, when the roots are kept at a low temperature, and also when the substratum is a bog soil. But when both the last named conditions are allowed to act together the response is the same in direction and amount as in dry mineral soils. The changes occurring in these leaves are very similar in their nature to those just described for *Stigeoclonium*. From an ecological standpoint, the palmella form of the alga is extremely xerophilous in character, while the filamentous form lies at the other extreme. It appears that we have here two very widely different plants, both of which respond to these various conditions in the same way.

#### SUMMARY.

The results of this series of experiments are as follows:

1. There are chemical substances, in at least some bog waters, which affect *Stigeoclonium* as do poisoned solutions and solutions of high osmotic pressure.

2. The responses of this alga to bog water and to cold are as nearly identical with those obtained by TRANSEAU with *Rumex*, for the same conditions, as the nature of the two plants would permit.

3. The active substances are not directly related to the acidity of the water.

4. Boiling the water decreases its acidity but does not appreciably affect its action as a stimulating agent.

5. The stimulating substances are most markedly present in water from those swamps whose vegetation is most definitely of the bog type. They are absent from river swamps and large lakes; in water from swamps whose vegetation is of a character intermediate between those of the river swamp and the bog, they are present to some degree, their amount being roughly proportional to the extent of the xerophilous character of the vegetation.

6. The stimulating substances here demonstrated may play an important rôle in the inhibition from bogs of plants other than those of xerophilous habit.

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## AN APPARATUS FOR OBSERVING THE TRANSPIRATION STREAM.

OTTO V. DARBISHIRE.

(WITH TWO FIGURES)

THERE are, roughly speaking, two sets of experiments by means of which we can investigate the presence of the transpiration stream in small plants. One of these is concerned with the root of the plant and with the demonstration of the phenomenon known as root pressure. The other set deals with the shoot and the suction exerted by it on the water which is being absorbed by the root.

We all know what happens when we fix some kind of root pressure apparatus to the stump of a small plant, like a fuchsia for example. Water will soon be pressed out of the stump with sufficient force to raise a column of mercury to a considerable height. We can at the same time attach to the shoot of the very plant used for the root pressure experiment some form of potometer. We will observe suction and a column of mercury can be raised to a considerable height thereby. Do these two separate experiments really—even approximately—show what was going on in the plant at the time the experiment was set up? I think the answer must be no. When the plant in question was cut across, the stump exhibited the phenomenon of pressure, but the shoot that of suction at the same level. It is obviously impossible that pressure and suction should be exhibited by an intact plant at the same level. It must be mentioned here, however, that if the two experiments are set up very quickly, we may find the stump exhibiting suction for a short time. This changes to pressure when the stump is saturated with water. The root may of course become saturated in a few minutes by simply being exposed to water during the setting up of the experiment. We do not therefore get a clear idea of what is going on in the plant, when we isolate the shoot from the root, by attaching to each one a separate apparatus.

In order to learn more about the relation between shoot suction and root pressure it is obviously necessary not to separate the two

portions of the plant entirely, but rather to keep them connected by some continuous bit of apparatus, so that, although the plant be cut in two, the shoot suction may still act on the root or the root pressure on the shoot. I use for this purpose a simple bit of glass apparatus, which I have called a *pinometer*. It will be necessary first to describe the apparatus; secondly, the way it is set up; and finally, to refer to a few of the experiments and the results obtained.

The pinometer consists of a straight bit of glass tubing (*fig. 1, b-d*), to which is obliquely attached by annealing on one side another short bit of glass tubing (*c-f*). On the opposite side a U-tube with an oblique connection is annealed on (*a-e*.) We have therefore four openings to this part of the apparatus (*a, b, c, d*). The bore of the glass tubing used for the pinometer depends entirely on the thickness of the stem of the plant used. The diameter of the glass tubes should about equal the diameter of the latter. A very convenient plant to use for demonstration purposes is a healthy fuchsia plant, not exceeding two feet in height.

The experiment should not be set up till all the various parts and tools are quite ready. The glass tubing should be cleaned to remove any greasiness, which is often the cause of introducing minute air bubbles into the system of tubes. The air should also be carefully removed from the rubber tubing. The more quickly everything is set up, the more nearly will the results obtained show what was going on in the plant at the time the experiment was made.

When everything is ready, the plant in its flowerpot is put into a bucket of water, so that it is immersed to a few inches above the point at which it is to be cut across. The leaves should not be moistened more than is absolutely necessary. The stem of the plant is now cut across under water in such a way that there is about one inch of stem, above and below the cut, devoid of buds or branches. If the stem has already a complete wood cylinder, the cortex may be removed with a sharp knife for about half an inch above the cut on the shoot, and below on the root.

The lower end of the shoot, without removal from the water, is fixed by rubber tubing to the opening *a*, *fig. 1*, and the portion *a-e* of the pinometer remains full of water, even when removed from the

water, and can be temporarily held by a clamp (*i*) on a retort stand.<sup>1</sup> Next some rubber tubing is slipped over the upper end of the root stump. This bit of tubing also fills with water and the whole flowerpot can now be removed. The end *b* of the pinometer is now quickly fixed to the rubber tubing over the stump. A gauge is securely attached to *c*, and water is poured into *d* from a small reservoir (*fig. 3, r*) till the whole system of tubes is full of water. Mercury is then poured into the outer limb of the gauge, and this causes water to pour out at *d*, to which some pressure tubing has been firmly fixed. When there is enough mercury in the gauge to give the columns sufficient play to rise and fall, the opening at *d* should be closed by a pinch-cock and the experiment is set up. Retort stands and clamps are used for keeping the various parts in position, and a millimeter scale (*k*) can be attached to one or both limbs of the gauge.

Should air make its appearance, it will collect under *d*, if it comes from any part of the plant except the lower end of the shoot. It can be removed from *d* by opening the pinch-cock and allowing water to run in from the reservoir. Should it accumulate under *a*, the shoot must be removed from the rubber tubing attaching it to the glass, and water allowed to enter the pinometer at *d* rather slowly. It will then be running out slowly at *a*, and the shoot is again fixed, the current of water preventing any air getting in.

In any case the removal of air means the opening of the pinch-cock at *d*, and this causes the mercury to go back to its starting point. This can be obviated by inserting a stop-cock between the oblique bit *j-c* (*fig. 1*) and the gauge. I do not however consider this necessary for the apparatus, which as described here is intended chiefly for qualitative and not quantitative observations.

The results obtained with the pinometer depend very much on the point at which we fix it in the plant. I will refer therefore to a few actual experiments, which I hope will show the value, however small, of the simple bit of apparatus just described.

In the first experiment to be described, a pinometer was fixed to

<sup>1</sup> For fixing the plant to the glass tube it is best, if possible, to employ some kind of pressure tubing. The latter can be made secure by tying with string or by employing some kind of clamp. The use of wire is to be deprecated.

the main shoot by cutting the stem a short distance above the lowest lateral shoot (*fig. 1*). After a very short time the mercury in the limb (*g*) of the gauge nearest the plant was seen to rise, as the latter was withdrawing water from the pinometer. As the mercury rises, the pull on the lower end of the shoot and on the upper end of the

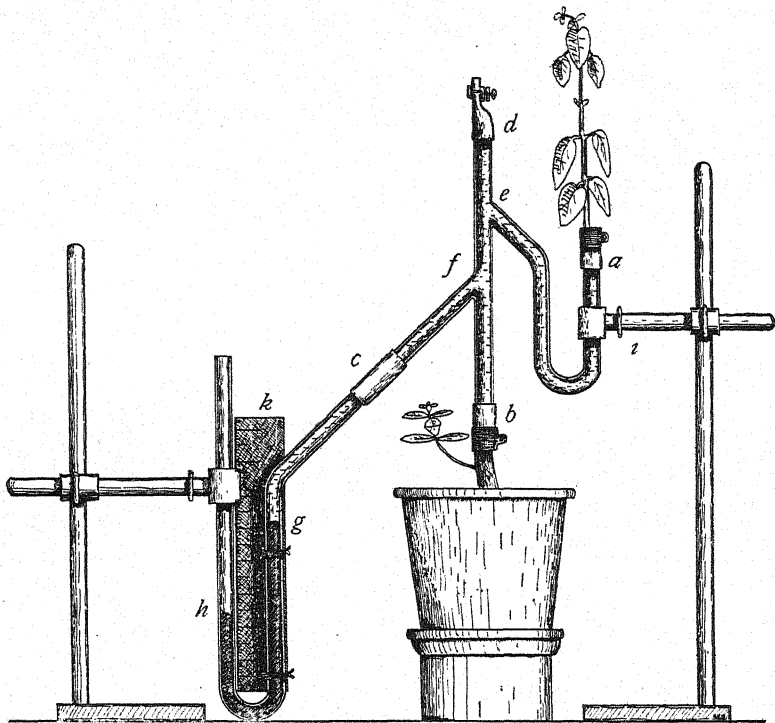


FIG. 1.—A fuchsia plant with one pinometer inserted just above the lowest lateral shoot: *a*, the attachment of the upper shoot; *b*, that of the root stump; *c*, the connection leading to the mercury gauge; *d*, the top opening of the pinometer, closed by rubber tubing and pinch-cock; *g*, the level of mercury in inner, *h*, that in outer limb of gauge; *k*, millimeter scale; the latter indicates shoot suction and the shoot at *a* is wilting; the stump at *b*, under pressure from the root, is flourishing.

root-end of the plant gets stronger, and gradually the leaves of the upper shoot wither. It will be noticed that the leaves of the lowest lateral shoot are quite fresh. Before the upper shoot dies altogether its axillary buds will generally develop and form small leaves, but even these succumb in the end.

In this experiment, therefore, and at the height in question, our plant exhibited shoot suction when tested by the pinometer. A modified barograph recording cylinder, made by NEGRETTI & ZAMBRA, was arranged to record the rise of the mercury in this particular experiment. A burette-float was placed on the mercury in the open end of the gauge (*h*). It was suspended by a fine thread, which ran over a pulley and was attached on the other side to the free end of a lever, the other end of which carried a pen which wrote on the revolving cylinder. The records taken during the first week showed that the water taken in from midday to midnight and that taken in from midnight to midday was in the proportion of three to two. Never did any pressure from the root, during night or day, cause the amount of water taken in to fall below nought.

In a second experiment a pinometer was fixed into a fuchsia plant about one inch above the soil and quite below the lowest lateral shoot. Root pressure manifested itself very soon and the mercury was forced out of the inner limb of the gauge, rising of course as rapidly in the outer one. In this case there was obviously pressure on the cut surfaces of shoot and root. The leaves of the shoot kept fresh as long as the pressure lasted, which was for sixteen days. On the sixteenth day there was a difference in the level of the mercury in the two limbs of the gauge of 20<sup>mm</sup>. Allowance however must be made for the column of water resting on the mercury in the inner limb of the gauge. After the sixteenth day the pressure was gradually reduced, very probably owing to the root becoming exhausted, its supply of organic food from the green leaves being cut off. The leaves began to wither as the pressure of the root decreased.

In a third experiment two pinometers were employed (*fig. 2*). One was fixed to the fuchsia plant just above the soil and the other just above the lowest lateral shoot. The plant was therefore cut into three parts, the lowest one of which, the stump, was devoid of any lateral shoots. The gauge attached to the lower pinometer ( $P_1$ ) very soon indicated pressure from the root, that of the upper pinometer ( $P_2$ ) suction from the two portions of the shoot. We have therefore in this experiment an arrangement by which root pressure and shoot suction can be observed at the same time. The difference in the appearance of the leaves on the two portions of the shoot is very



striking. The leaves of the upper shoot are dead, there being a strong pull on the lower end. The leaves of the middle shoot are flourishing, there being a push on its lower end, although the lower pinometer is separated from the upper one by about two inches of stem only

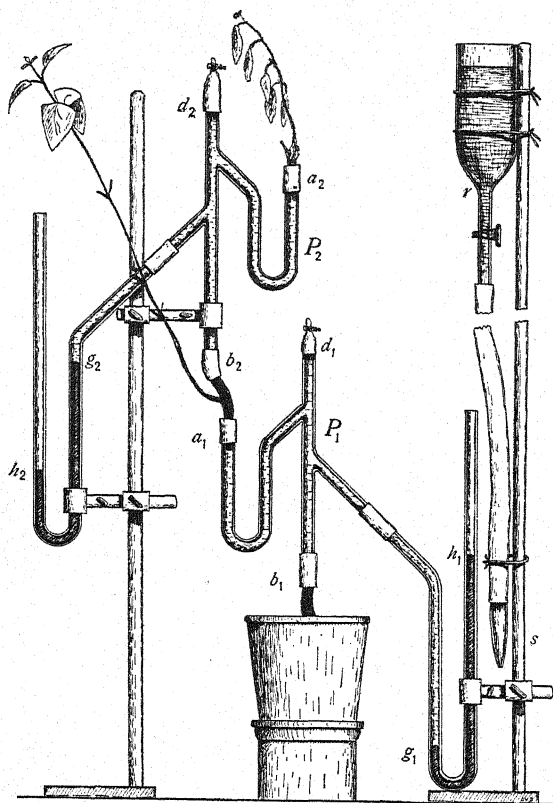


FIG. 2.—A fuchsia plant with two pinometers: the lettering as in fig. 1; the lower pinometer ( $P_1$ ) shows root pressure and its shoot ( $a_1$ ) is flourishing; the upper one ( $P_2$ ) exhibits shoot suction, and its shoot ( $a_2$ ) is wilting;  $r$ , reservoir of water,  $s$ , its spout.

(between  $a_1$  and  $b_2$ ). A fortnight after being set up, a reading for this experiment showed a difference in level of the two columns of mercury of  $18^{\text{mm}}$  in the lower pinometer, indicating pressure from the root, and a difference of  $20^{\text{mm}}$  in the upper pinometer, indicating suction from the shoot.

An experiment was also made with three pinometers inserted into the stem of a fuchsia plant. The following readings were taken after the experiment had been going on for some time. The lower pinometer showed root pressure with a difference in the level of the mercury columns of  $31^{\text{mm}}$ , the middle pinometer showed suction with a difference in level of  $85^{\text{mm}}$ , and the upper pinometer suction with a difference of  $63.5^{\text{mm}}$ . The figures for the next day in millimeters were 39 (an increase of 8), 127.2 (42.2), and 128 (64.5) respectively. The two lower pinometers were below the lowest branches. In this case, therefore, root pressure could not be observed even up to the lowest lateral shoot. As in all the previous experiments, suction, where observed at all, was maintained day and night, till, owing to the pull on the cut surface of the plant, air made its appearance and the mercury returned to its original level.

The pinometer, as described here, is meant to be of use chiefly for class and demonstration purposes. I wish now to point out what the results obtained by employing it are, that is to say what observations can be made on the transpiration stream.

We can readily see that in our plants, at least, it is never a function of the root to press water up into the leaves. By day and by night the phenomenon of root pressure can be observed only below the lowest shoot. But root pressure is an extremely useful if not a necessary process by which the rise of the water is started. Referring to those of our experiments in which the lower cut surface of the shoot was exposed to pressure, we see that the plants do not suffer much by the stem being cut across. It appears to be necessary that water should be forced into the lowest end of the vascular system; or at least there should be no pull on it. Root pressure, therefore, is not only a symptom of the avidity with which the roots are absorbing water, but it is of importance as assisting in the starting of the transpiration current.

It must be mentioned here, however, that the insertion of a pinometer into a fuchsia plant is in any case a serious thing for the latter. The phenomena of exudation and bleeding seem to cease entirely when the shoot has been severed from its connection with the root. This statement holds good whether the gauge of the pinometer shows pressure or suction. The fact that at different heights in the plant

we get readings which at least show that the pressure may vary very much in even two or three inches of stem, is a proof, I think, that the "atmospheric pressure" theory of the rise of water is not correct.

When we get away from the root we find the phenomenon of shoot suction manifesting itself. In fact, as already pointed out, shoot suction generally seems to be stronger than the pressure from the root at any point except just above the root. That is to say, the shoot is able at any time to take in more water than can be supplied by the root. Numerous experiments show that this is the case in winter and summer, day and night, in the plants I experimented upon.

Which part of the plant is exerting this suction? I have spoken here of shoot suction, but it is possible to split up this part of the transpiration stream into two distinct processes, namely the leaf suction and the wood lift. There is not much mystery about the former. We can understand how the water is removed from the finest endings of the vascular system. If, however, we remove the leaves from a shoot which has been attached to a pinometer or even cut off the upper part bearing leaves, leaving only a short leafless shoot stump, we still get water rising in the wood and exerting a pull on the gauge of the pinometer. The activity of the leaves simply removes the water from the top of the vascular system, and this water is replaced by a process going on in the wood.

I am mentioning this simply to show that in the experiments with the pinometer the taking in of water by the shoot is not a phenomenon of leaf suction but one of wood lift. The force of the wood lift is very great; it is generally greater than the root push. But, as our experiments show, it cannot act efficiently for any length of time if the lowest end of the vascular system is exposed to a pull from below. It is as yet not known how the wood lift acts. It is therefore all the more necessary to make as many observations as possible on this process. I think the pinometer does make it possible to observe at least one property of this water current. It is continually in a state of what is known as "negative pressure." A natural result of this is that the air, which the water absorbed by the plant contains under ordinary atmospheric pressure conditions, escapes from the water when inside the plant. Over and over again my experiments have been brought to an end by air collecting, generally under the shoot. Air-bubbles

are bad for the conducting of the experiments, and the more they are kept out the more water is absorbed by the plant when attached to a pinometer. It is obvious that the plant must also guard against the accumulation of air in the column of water which fills the vascular system. No doubt this will in part account for the peculiar structure of the wood elements. Do the latter bear any relation in their structure to the nature of the water generally found in the localities in which the plant grows?

The form of pinometer mentioned in this paper is intended, as already mentioned, essentially for demonstration purposes. It is possible by its use to observe, more clearly than hitherto, the relation between shoot suction and root pressure. Owing to the preliminary nature of this paper I have refrained from giving any lengthy readings taken during the experiments. Their value in any case would not be very great, being taken with the simple form of pinometer here described. A more elaborate bit of apparatus is therefore in course of construction, by which any air making its appearance in any part of the pinometer is removed automatically at regular intervals without altering the conditions of pressure inside the system of tubes. Furthermore, it is connected with an automatic recording instrument, in which the difference in the height of the two mercury columns will be reduced as much as possible.

The nature of this paper, I hope, will excuse my having made no reference to any literature. It was not my intention to discuss the old or bring forward a new theory with regard to the rise of water. We still have the suction by the leaves, the pressure by the root, and the as yet little understood lifting of the water by the wood. In writing this paper, it was my object to give an account of a very simple bit of apparatus, by means of which various phenomena connected with the transpiration stream in small plants could be readily observed. I hope later on to be able to publish some more detailed observations on the properties of the wood lift, taken by more elaborate instruments.

Diagrams illustrating the working of the pinometer were shown at the last Cambridge meeting of the British Association.

UNIVERSITY OF MANCHESTER, ENGLAND.

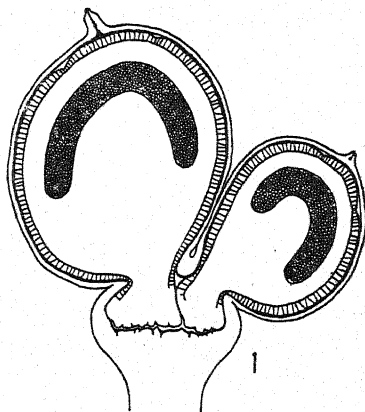
## BRIEFER ARTICLES.

### POLYEMBRYONY IN SPHAGNUM.

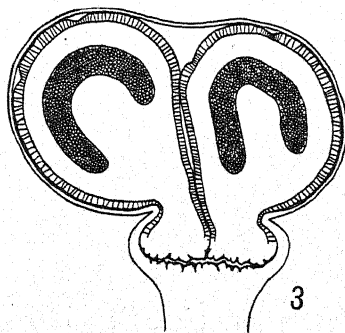
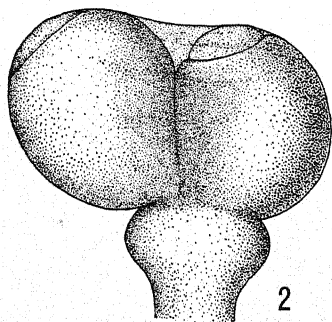
(WITH THREE FIGURES)

DURING July 1904, while collecting sporophytes of *Sphagnum* for class use, the writer discovered the peculiar specimens described in this note. The particular species of *Sphagnum* has not been determined, but it is a large variety which grows abundantly in the swamps around Tower, Minnesota.

Among the thousands of sporophytes handled, five cases were found where in two archegonia at the end of the same branch the oospheres had been fertilized and each oosperm had developed into a normal sporophyte. In these specimens each capsule was enclosed by its separate calyptra and the haustra of each two sister sporophytes were inserted side by side in the bulbous end of the pseudopodium (*fig. 1*).



Two cases were also found where two sporophytes had developed in the venter of one archegonium (*fig. 2*). They were more or less distorted



and modified by mutual pressure, but each presented the essential structure of a normal sporophyte (*fig. 3*). When studied in sections, the tissue of

each sporophyte appeared to be entirely independent of that of its twin except in the loose tissue forming the base of the haustria, where the line of separation was not clearly recognizable in all sections. In the region of contact, the epidermis, while quite distinct, was less strongly developed than on the free faces. Since the sporophytes were nearly mature at the time of collection, it was impossible to determine the conditions which led to the production of twins. It is probable that two functional oospheres were produced in the venter of each archegonium, although it is not impossible that twinning took place through an early branching of the young protocorm.—HAROLD L. LYON, *University of Minnesota*.

### ADENODERRIS, A VALID GENUS OF FERNS.

(WITH TWO FIGURES)

THE genus *Polystichum*,<sup>1</sup> typified by the well-known *P. Lonchitis* constitutes a natural and well-defined group of ferns and has commonly had general recognition, recently even by American writers.<sup>2</sup> Its species are characterized, briefly, by their rigidity and erect habit, smooth firm dryish texture, mainly auriculate and spinulose or mucronate divisions, abundant chaff, free venation, and ordinarily by the orbicular centrally peltate indusia. The genus was divided by JOHN SMITH into two sections: the one, typified by *P. aculeatum* and *P. Lonchitis*, with fasciculate generally erect acaulose veneration; the other, typified by *P. coriaceum*, with uniserial sarmentose veneration. In view of that writer's natural bent for generic segregation along the very lines on which the species of this genus were placed in two sections, it would not have been surprising if he had accorded to each section generic rank. That such a disposition—in view of the two radically different types of veneration—was not made is significant, for it emphasizes SMITH's belief that in other respects the species are in too close agreement to warrant their division into two genera. There is, however, variation in one other particular; in certain species of both groups the indusium is caducous, or, as in *P. tenue*,<sup>3</sup> apparently quite wanting; but even in these cases the appearance of the plants is so unmistakably that of *Polystichum* and their agreement in the main particulars so essential that a rational course seems to necessitate their recognition as true members of the genus. We have thus a group of species which, though offering

<sup>1</sup> ROTH, Teut. Fl. Germ. 3:69. 1800.

<sup>2</sup> GILBERT, in papers presented at the Boston Meeting (1898), 22. 1899. UNDERWOOD, Our native ferns, ed. 6, 115. 1900. DAVENPORT, Rhodora 4:9. 1902, etc.

<sup>3</sup> GILBERT, Fern Bull. 8:63. 1900.

variation in two lines, is nevertheless, in the characters enumerated at the beginning of this paper, one of the most unified to be found among the ferns. Indeed, as GILBERT has remarked, the general characters of the genus are so distinctive and obvious that the descriptive term *polystichoid* has come into rather common use.

The historic treatment of *Polystichum*, although of much interest, need not be here discussed at length. The genus has been made often to include diverse groups not properly associable with its typical members; and in several cases it has been an author readiest to admit numerous small genera who has failed to realize the essential unity of the group and to refuse to admit unlike forms. Thus MOORE retained *Cyclopeltis* J. Sm. under *Polystichum*, though it constitutes a most distinct natural genus. And more recently, DIELS,<sup>4</sup> while properly removing *Cyclopeltis*, nevertheless allows *Phanerophlebia*, *Cyrtomium*, and *Adenoderris* to remain within the genus. *Cyrtomium* and *Phanerophlebia* have recently been held distinct from each other and from *Polystichum* by UNDERWOOD,<sup>5</sup> and it now appears certain that *Adenoderris*, long ago founded by JOHN SMITH upon the anomalous *Aspidium glandulosum* of Hooker and Greville, represents a perfectly valid genus. The discovery of a second species of *Adenoderris* with very different venation, from Guatemala, is of interest and has seemed to render desirable the present notice of the genus and its relationship.

ADENODERRIS J. Sm. Hist. Ferns 222. 1875.<sup>6</sup>—Small plants of lax habit, distinct from *Polystichum* by their herbaceous texture, aspinulose margins, and dense glandular-pilose covering.—Type, *Aspidium glandulosum* Hook. and Grev. from Jamaica. Species two.

*Adenoderris viscidula* (Mett.).—*Aspidium glandulosum* Hook. and Grev. Icon. Fil. 2: pl. 140. 1831; not *Aspidium glandulosum* Blume, Enum. Pl. Javae 2: 144. 1828. *Adenoderris glandulosa* J. Sm. Hist. Ferns 223. 1875. *Aspidium viscidulum* Mett. Abhand. Senck. Nat. Gesells. 2: 322. 1858.—The species was very fully characterized upon specimens received from several collectors in Jamaica and is the subject of an excellent illustration by HOOKER and GREVILLE. Lately it has been well described by JENMAN.<sup>7</sup> SMITH, basing his genus upon the single species, published the

<sup>4</sup> DIELS, in Engler and Prantl, Die natürlichen Pflanzenfamilien 14: 183-189. 1899.

<sup>5</sup> UNDERWOOD, Bull. Torr. Bot. Club 29: 121-136. 1902. See also UNDERWOOD in Bull. Torr. Bot. Club 26: 205-216. pls. 359-360. 1899.

<sup>6</sup> The genus seems to be published here for the first time, although the author cites the date 1852.

<sup>7</sup> Bull. Bot. Dept. Jamaica 2: 197-198. 1895.

following characters: "Vernation fasciculate, erect, acaulose. Fronds 6 to 8 inches in length, oblong, lanceolate, pinnatifid, densely covered with pilose glands, decurrently attenuated to a short stipe. Veins pinnately forked. Receptacles punctiform, medial. Sori round. Indusium orbicular, occasionally reniform."<sup>8</sup> In habit the plant was said to be "totally at

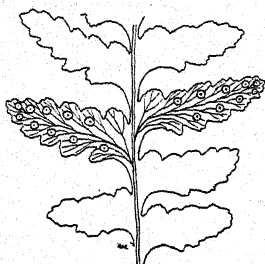


FIG. 1.—*Adenoderris viscidula* (Mett.) Maxon; natural size.

variance" with any species of *Polystichum*, and this opinion was formed entirely from herbarium specimens. An examination of material in the field indicates even more plainly how inappropriate has been the usual systematic association of this peculiar plant with true members of *Polystichum*. The fresh plants are spongy, very lax, and intensely viscid, and except for the peltate indusia have nothing to suggest a close relationship with the stiff smooth spinulose *Polystichums*. The venation of *A. viscidula*, which was not indicated by

HOOKER and GREVILLE, is shown in *fig. 1*, which represents the middle portion of a Jamaican specimen (*Clute* no. 333; U. S. National Herbarium, no. 349588). This feature and the position of the sori are discussed under the next species.

*A. viscidula* is known only from Jamaica and Cuba. JENMAN states that in Jamaica it occurs upon "rocky banks and skirts of forests 1500–3000<sup>ft</sup> altitude; plentiful in one place at least between Gordontown and Guava Ridge. There is, however, but one sheet in the Jenman Herbarium at New York. Other Jamaican specimens are: *Clute* no. 333, collected above Gordontown, March 12, 1900, at an altitude of 450<sup>m</sup>; *Underwood* no. 2498, collected near the Green River (below Cinchona), April 22, 1903, at an altitude of 750<sup>m</sup>; and specimens collected by *D. E. Watt* at or near the last locality in May 1903. The Cuban record<sup>9</sup> is based upon *C. Wright* no. 1052. Specimens of this number in the D. C. Eaton herbarium are identical with the Jamaican plant; to them is attached Wright's original label stating that they were collected in rocky ravines on mountain sides near Josephine, October 25 (1859).

***Adenoderris sororia*, sp. nov.**—A delicate plant of small size, the fronds glandular throughout. Rhizome slight, erect, having long fibrous rootlets rather thickly clothed with delicate bright brown chaff: fronds 8<sup>cm</sup> long, short-stipitate, spreading, oblong-lanceolate, deeply pinnatifid, with about

<sup>8</sup> Only orbicular indusia have been observed by the writer.

<sup>9</sup> Hooker, *Sp. Fil.* 4:6. 1842.



ten pairs of usually subopposite to alternate pinnae; pinnae ovate to deltoid, the middle ones 10–13<sup>mm</sup> long, the lowermost scarcely reduced, all deeply divided into about three blunt lobes upon both upper and lower margins, each lobe usually once soriferous near the outer side at the base, the sorus being borne at the *extremity* of a spur given off from the otherwise usually simple single veinlet; venation terminating well within the lobe; indusium minutely glandular, orbicular, centrally peltate.

Founded upon no. 868 of *John Donnell Smith's* Guatemalan plants; said to have been collected by *von Türckheim* at Sesisp, Department of Alta Vera Paz, altitude 1200<sup>m</sup>, March 1886, and distributed as *Aspidium glandulosum*. The most perfect material of this number the writer has seen is that preserved in the D. C. Eaton herbarium at Yale University, and this, having served for the accompanying illustration (*fig. 2*), may stand as the type, though the specimens in the United States National Herbarium and the herbarium of the New York Botanical Garden are of the same collection. Captain SMITH has stated (in litt.) that duplicates were presented also to the W. M. Canby, Philadelphia Academy, Kew, Berlin, Paris, and DeCandolle herbaria.

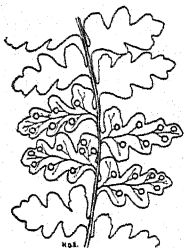


FIG. 2.—*Adenoderris sororia* Maxon, n. sp.; natural size.

*Adenoderris sororia* is distinct in all states from *A. viscidula*, though in its lax habit, slight texture, aspinulose margins, and glandular covering it shows an undoubted generic alliance with that species. It differs specifically in its less size, bipinnatifid condition throughout (*A. viscidula* though larger is only deeply once-pinnatifid), more sparse glandular covering, and in its spreading simpler *included* venation, the sori being borne terminally at the apices of the veinlets. In *A. viscidula* the veinlets are pinnately forked and excurrent to the suberose margins, the sori being borne *dorsally*, *i. e.*, upon the veinlets and at some distance from the margin. These differences, while very marked, appear to be no more than specific, and SMITH's original generic diagnosis quoted above must therefore be amended as regards venation.

Both drawings, which are by Mr. H. D. HOUSE, are natural size. That of *A. sororia* represents parts of the third, fourth, fifth, sixth, and seventh pairs of pinnae of a frond of the type specimen.—WILLIAM R. MAXON.

## CURRENT LITERATURE.

### BOOK REVIEWS.

#### Rusts of Switzerland.

THREE NOTABLE WORKS on plant rusts have appeared within a year: KLEBAHN'S *Wirthswechselnde Rostpilze*, the first volume of SYDOW'S *Monographia Uredinearum*, and FISCHER'S *Die Uredineen der Schweiz*. Each of these works covers a distinct field, and in its own way marks advance in the elucidation of the world's rust flora, and in an understanding of the problems connected therewith. The last named work,<sup>1</sup> although embracing a limited region, is conceived upon such a broad plan, and carried out with so much completeness, that it serves as the best model yet produced for a uredineous manual.

A large number of the species found in Switzerland are cosmopolitan. Every species is described in detail, and with few unavoidable exceptions direct from specimens, and is also illustrated with outline drawings. The descriptions are especially full, embracing not only the usual characters, but those derived from the pycnidia, the peridial cells, and the germ pores. The illustrations are drawn to a uniform scale, and are skilfully made. Often a dozen or more teleutospores are shown. Usually uredospores are included, and always drawn in a normally upright position, a most commendable innovation. In most cases a transverse section of two or more peridial cells shows their varying thickness of wall and sculpturing, another helpful innovation.

The notes which follow the diagnoses, briefly stating how much is known of the life history of the species, are helpful and suggestive. The list of Swiss stations for each species is more especially of local value to collectors.

The systematic arrangement is essentially that of DIETEL in ENGLER and PRANTL'S *Pflanzenfamilien*. Under the genera the species are distributed by hosts and morphological characters, with a view to showing relationship. A general key on the same basis is provided, together with excellent indexes, and a full modern bibliography.

Three chapters are of unusual interest to the general mycologist. In one the distribution of the Uredineae in Switzerland is analyzed and discussed, taking into account the ecological factors controlling the hosts. In another the general classification and the grouping of species within the genera are considered in the light of the most probable hypotheses regarding the phylogenetic descent of the rusts. And in the third the difficult questions regarding the value of various morphological and biological characters for discrimination of species are presented.

<sup>1</sup> FISCHER, ED., *Die Uredineen der Schweiz*. Beitr. z. Kryptogamenflora der Schweiz. II<sup>2</sup> imp. 8vo. pp. xciv + 590. figs. 342. Bern: J. K. Wyss. 1904. 20 francs.

This work by Dr. FISCHER, for which he has been preparing for more than a dozen years, is replete with new matter of great value and is altogether admirable.—J. C. ARTHUR.

#### MINOR NOTICES.

THE FOSSIL FRUITS from the lignites of Brandon, Vermont, are the subject of an important contribution by PERKINS.<sup>2</sup> In 1861 LESQUEREUX described twenty-one species from this locality, which he regarded as of approximately the same age as the Eningen stage of the Swiss Miocene. In 1902 KNOWLTON published a brief paper of forms from this locality which represents all we knew of this interesting flora up to the time of publication of the present paper. The deposits have been much obscured and inaccessible for a half century, until the coal famine of 1902, when the lignite came into demand locally as a substitute for coal. The state geologist, GEORGE H. PERKINS, was enabled to secure a magnificent collection of the fossil fruits during the mining operations, and the present paper contains the result of preliminary study of these collections. One hundred and eighteen species are recorded, and many new forms of more or less doubtful botanical affinities are described. These are largely included in the following new genera: *Monocarpellites* (11 spp.), *Hicoroides* (5), *Bicarpellites* (5), *Brandonia*, *Rubioides*, *Sapindoides* (6), and *Prunoides*. The illustrations consist chiefly of photographs of type specimens, which are perhaps less satisfactory in showing details than careful drawings. The flora is unique in the abundance and variety of its fruits, and it is to be hoped that future study by Dr. PERKINS will demonstrate with more precision the exact age of the formation containing them. The accompanying clays should be searched for leaf remains.—EDWARD W. BERRY.

POPULAR ACCOUNTS of soil inoculation for legumes devised by MOORE have attracted wide attention, so that it is of special interest to receive his own account.<sup>3</sup> The nitrogen is fixed by the tubercle-forming bacteria within their bodies. This was determined by cultures in flasks containing nutrient solutions without nitrogen. There was no increase of nitrogen in the solution, but a marked increase in the organisms themselves. In its biology the organism is therefore considered a parasite. Later the plant is able to overcome the parasite and profit by the nitrogen which has been fixed. When grown on nitrogenous media, it was found that the organism lost both its power of infecting leguminous plants and its power of fixing nitrogen. In non-nitrogenous media both of these properties were retained. The failure of NOBBES's attempts in Germany a few years ago to put upon the market pure cultures of this organism can probably be attributed to lack of recognition of this fact. As a result of these studies MOORE has devised

<sup>2</sup> PERKINS, GEO. H., Description of species found in the Tertiary Lignite of Brandon, Vermont. Rept. State Geologist, Vt. 1903-1904. pp. 174-212. pls. 75-81. 1904.

<sup>3</sup> MOORE, G. T., Soil inoculation for legumes, etc. U. S. Dept. of Agric., Bureau of Pl. Industry, Bull. 71, pp. 72. pls. 10. 1905.

a method of putting up for distribution pure cultures of *Pseudomonas radiculicola*, grown in nitrogen-free media and dried on cotton immersed in the culture. These cultures are sent out by the U. S. Department of Agriculture together with packages of nutrient salts to multiply the organism. The mass-culture thus obtained is used to inoculate the seed or the soil. Numerous reports from farmers of all states indicate that this method will prove successful and practicable.—H. HASSELBRING.

THE OFFICE of Experiment Stations of the U. S. Department of Agriculture has recently issued a valuable syllabus<sup>4</sup> of the diseases of the Irish potato in the United States by STEWART and EUSTACE of the New York (Geneva) Experiment Station. This is the second of a new series of publications designed primarily to assist farmers' institute lecturers in the presentation of various important subjects to farmers. Each lecture is accompanied by a set of lantern slides, there being in this case forty-seven slides in the set. Arrangements have been made to loan these slides to lecturers, or they may be purchased through the Department of Agriculture at a very moderate cost. Both the syllabus and the accompanying set of slides should prove of great value to teachers of plant pathology in presenting the diseases of the potato. A brief bibliography is appended to the syllabus, which contains references to the most important American literature of this subject.—E. MEAD WILLCOX.

AN UNDATED EDITION of ANDREWS'S *Botany all the year round* has been issued, which differs from the preceding one<sup>5</sup> only in being bound into one volume with a flora by W. NEVIN GEDDES.<sup>6</sup> This flora brings together compact and simple descriptions of the more common flowering plants, not only native and naturalized, but also cultivated, and includes about 1,250 species. The sequence of families is an interesting reminiscence of the old time classification, and it is quite a pleasure to see gymnosperms once more as a subclass of "Exogens or Dicotyledons." The nomenclature, too, is frankly "conservative and eclectic;" but the book does as well as any other to enable a student to find names for plants, which seems to be regarded as a very valuable exercise.—J. M. C.

THE FOURTH PART of SARGENT'S *Trees and shrubs*<sup>7</sup> contains plates and descriptive text of species of *Acer* (13), *Parthenocissus* (3), *Malus*, *Oroxylum*, *Phellodendron* (3), *Arctostaphylos* (2), *Dracaena*, and *Pinus* (2). There are

<sup>4</sup> STEWART, F. C. and EUSTACE, H. J., Syllabus of illustrated lecture on potato diseases and their treatment. Office of Exp. Stat. U. S. Dept. Agr. Farmers' Inst. Lecture 2:1-30. 1904.

<sup>5</sup> See BOT. GAZETTE 35:439. 1903.

<sup>6</sup> GEDDES, W. NEVIN, A brief flora of the eastern United States. New York, Cincinnati, Chicago: American Book Company, with no date.

<sup>7</sup> SARGENT, C. S., Trees and shrubs. Illustrations of new or little known ligneous plants, prepared chiefly from material at the Arnold Arboretum of Harvard University. Part IV. pp. 151-217. pls. 76-100. Boston and New York: Houghton, Mifflin & Company. 1905. \$5.00.

two new Chinese maples, a conspectus of the maples of eastern continental Asia, two new American species of *Parthenocissus*, and one new Chinese *Oroxylum*, by ALFRED REHDER; a new *Phellodendron*, by CHARLES S. SARGENT; two new Californian species of *Arctostaphylos*, by ALICE EASTWOOD; a new Central American *Dracaena*, by JOHN DONNELL-SMITH; and two new Mexican pines by G. R. SHAW. This part closes the first volume, and contains the title-page, index, and corrections.—J. M. C.

HERBERT STONE<sup>8</sup> has brought together a most interesting collection of descriptions and excellent photomicrographs of commercial timbers. Being able to draw upon the British colonies for material, the list is unusually full. An introductory chapter gives a general account of the varying structure of wood from the standpoint of one who has a practical acquaintance with timber; and this is followed by practical hints as to its identification. The list of timbers includes 247 numbers, each species with a very full description, all the genera being illustrated by photomicrographs.—J. M. C.

THREE PARTS of an illustrated handbook of the angiospermous woody plants native or hardy in middle Europe by C. K. SCHNEIDER have appeared.<sup>9</sup> The illustrations are numerous and excellent, floral dissections, fruits, and leaves being given, and in many cases fine half tones of characteristic bark. The ENGLER and PRANTL sequence is used. The first part includes *Salicaceae* to *Fagaceae*, with 95 illustrations; the second part, *Fagaceae* (*Quercus*) to *Berberidaceae*, with 102 illustrations; the third part, *Berberidaceae* to *Spiraceae*, with 90 illustrations.—J. M. C.

A SECOND EDITION of GROUT'S *Mosses with a hand lens* has been published,<sup>10</sup> including the common liverworts. The review of the first edition<sup>11</sup> stated the general scope and purpose of the book. The demand for a new edition has justified the undertaking, and with the addition of much new material the author believes that he has reached the limit of the hand lens. The addition of the common liverworts represents a very natural extension of the author's method, and introduces beginners to a group they must have encountered repeatedly in collecting mosses.—J. M. C.

<sup>8</sup> STONE, HERBERT, *The timbers of commerce and their identification*. Illustrated with 186 photomicrographs by Arthur Deane. Imp. 8vo. pp. xxxviii+311. London: William Rider & Son. 1904.

<sup>9</sup> SCHNEIDER, CAMILLO KARL, *Illustriertes Handbuch der Laubholzkunde*. Charakteristik der in Mitteleuropa heimischen und im Freien angepflanzten angiospermem Geholz-Arten und Formen mit Ausschluss der Bambuseen und Kakteen. Jena: Gustav Fischer. 1904. Each part M4.

<sup>10</sup> GROUT, A. J., *Mosses with a hand lens*. A non-technical handbook of the more common and more easily recognized mosses of the northeastern United States. Illustrated by MARY V. THAYER. Second edition, revised, enlarged, and including the hepatics. 8vo. pp. xvi+208. pls. 39. figs. 118. New York: The Author, 360 Lenox Road, Flatbush. 1905.

<sup>11</sup> BOT. GAZETTE 31:132. 1900.

NUMBERS 221 and 222 of ENGLER and PRANTL's *Pflanzenfamilien* have appeared, the former containing a continuation of the lichens by A. ZAHLBRUCKNER, the latter a continuation of the mosses by V. F. BROTHERUS.—J. M. C.

THE SEVENTH FASCICLE of DALLA TORRE and HARMS's *Genera Siphonogamarum*<sup>12</sup> has just appeared, including genera from Acanthaceae (7938. *Echinacanthus*) to Compositae (9371. *Liabum*).—J. M. C.

#### NOTES FOR STUDENTS.

PALEOBOTANICAL NOTES.—BRABENEC<sup>13</sup> records thirteen species of plants from a new locality, Holedeč, in the Saaz basin of northern Bohemia, describing new species in *Carya*, *Acacia*, *Paliurus*, and *Porana*.—BERRY<sup>14</sup> describes additional material from the Cretaceous near Cliffwood, N. J., consisting of rather fragmentary remains of nine additions to that flora, making the total number of known forms ninety-five.—The same author describes<sup>15</sup> a new palm, represented by abundant but fragmentary remains of leaves, from the mid-Cretaceous of the coastal plain in Delaware and Maryland.—In notes on Tertiary plants PENHALLOW<sup>16</sup> describes wood of *Taxodium* and *Thuja* from the basal Eocene of Alberta, and of *Cupressoxylon* from the Cretaceous of Assiniboia. Wood of *Pseudotsuga Douglasii* is identified from near Bozeman, Montana, and the characteristic Pleistocene *Larix americana* (*Larix laricina*) is identified from Georgia. The latter find is most interesting, showing as it does that the larch had pushed about 480 miles farther south than its present southern limit during the Scarborough period of the Glacial. Wood of *Pinus rigida* is recorded from the Pleistocene of New York; and *Juniperus californica* and *Pseudotsuga macrocarpa* are recorded from the Pleistocene at Orleans, Humboldt county, California. The paper concludes with an enumeration of a number of species, based on leaves and wood, from the well-known Don River Pleistocene of Canada.—WHITE<sup>17</sup> has a paper on "Fossil plants of the group Cycadofilices," in which the chief points of interest in this most interesting group are enumerated. He concludes, with WILLIAMSON, that secondary wood originated, polyphyletically and polychronously, as an engineering feature. It is suggested that the heterosporous filicean ancestors of the group Pteridospermae will be found in the lowest Carboniferous if not in the Upper Devonian. Should the author's *Kalymma grandis* prove to

<sup>12</sup> DALLA TORRE, C. G. DE, and HARMS, H., *Genera Siphonogamarum ad systema Englerianum conscripta*. Fasc. 7. pp. 481-560. Leipzig: Wilhelm Engelmann. 1905. M6.

<sup>13</sup> BRABENEC, F., Ueber einen neuen fundort v. Tertiären Pfl., etc. v. Saazer Schichten Bull. Inter. Acad. Sci. Bohême, 1904. pp. 8 pl. 1.

<sup>14</sup> BERRY, E. W., Bull. Torr. Bot. Club 32:43-48. pls. 1-2. 1905.

<sup>15</sup> BERRY, E. W., *Torreya* 5:30-33. figs. 2. 1905.

<sup>16</sup> PENHALLOW, D. P., Trans. Roy. Soc. Can. II. 10:57-76. 1904.

<sup>17</sup> WHITE, DAVID, U. S. Geol. Surv. Professional Paper No. 35: pp. 35-84. pls. 2-6. 1905.

be pteridospermic, as is expected, it will serve to emphasize the evidence of the fossil wood (*Dadoxylon*) as to the occurrence of gymnospermous-like plants in the middle Devonian (Genesee), a time nearly as remote as that furnishing the oldest known ferns of undoubted authenticity, and would seem to render the search for ancestral forms of these comparatively highly organized pteridospermic types futile.—The same author gives<sup>18</sup> a systematic account of the Devonian flora of the Perry basin, Maine, listing twenty-nine species, not including nine more or less doubtful species which DAWSON reported from this locality. Several new generic and specific types are described, and numerous nomenclatorial points are cleared up. The paper is fully illustrated.—EDWARD W. BERRY.

CLAUSSEN<sup>19</sup> gives an account of the life history of the ascomycete *Boudiera*. The sexual organs consist of short filaments which are developed in clusters and become very much twisted together, presenting spirally wound structures somewhat resembling the sexual organs of *Gymnoascus*. These filaments are differentiated into antheridia and ascogonia which fuse. After fertilization a cluster of short ascogenic hyphae arise that develop a small group of asci which become loosely enveloped by surrounding paraphyses from sterile portions of the mycelium. The female organ is the thicker filament of the two and consists of an ascogonium, containing several nuclei, which bears a terminal sterile cell, perhaps two. The nuclei in the sterile cell break down, and it finally becomes the medium (conjugation tube or trichogyne) through which the protoplasm from the antheridium enters the ascogonium. The antheridial filament is thinner and also contains several nuclei, which after the fusion with the sterile terminal cell pass into the ascogonium. The fertilized ascogonium then contains some ten or twelve nuclei and the antheridial filament and sterile terminal cell are empty. The nuclei in the fertilized ascogonium fuse in pairs. The empty antheridial filament and sterile cell collapse. The fertilized ascogonium increases in size, the fusion nuclei become conspicuous, and it finally divides into several cells by cross walls. The ascogenic hyphae are very short and the tips take at once the form of a hook and contain four nuclei. One nucleus lies in the tip, another in the stalk, and the remaining two in the bent portion of the hook. The four-nucleate condition is derived from a two-nucleate, but the preceding history is not known. The pair of nuclei in the bent portion of the hook become separated by walls from the tip and base of the filament and shortly coalesce; this cell becoming then a young ascus containing the single fusion nucleus. Thus each ascogenic hypha develops a single ascus. The terminal cell remains indefinitely, but there is no development from it. Several asci are formed from one ascogonium, but not simultaneously. Their number is believed to agree with the number of fusion nuclei in the ascogonium. The process of spore formation appears to follow HARPER's account, but

<sup>18</sup> WHITE, DAVID, *Smithsonian Miscellaneous Coll.* 47:377-390. pls. 53-55. 1905.

<sup>19</sup> CLAUSSEN, P., *Zur Entwicklungsgeschichte der Ascomyceten Boudiera*. *Bot. Zeit.* 63<sup>1</sup>:1-28. pls. 1-3. 1905.

details are not given. The paper ends with a long historical discussion of the disputed sexuality of the ascomycetes and supports HARPER's conclusions.—B. M. DAVIS.

ITEMS OF TAXONOMIC INTEREST are as follows: T. MAKINO (Bot. Mag. Tokyo 18:156. 1904) has separated the Japanese form referred to *Croomia pauciflora* T. & G. as a distinct new species (*C. kiusiana*).—W. B. HEMSLEY (Hooker's Icon. Plant. IV. 8:pl. 2781. 1905) has named the type of a new West Australian genus of Compositae (Helichryseae) *Thiseltonia Dyeri*.—PH. VAN TIEGHEM (Jour. Botanique 19:45-58. 1905) has made the genus *Octocnema* (provisionally placed under Olacaceae) the type of a distinct family (*Octocnemeaceae*).—A. A. HELLER (Muhlenbergia 1:111-118. 1905) has described new Californian species of Ribes, Trifolium, and Stachys.—J. CARDOT (Bull. Herb. Boiss. 5:208. 1905) has described a new genus (*Alophosia*) of mosses from San Miguel.—L. RADLKOFER (*idem* 222) has described a new genus (*Sisyrolepis*) of Sapindaceae from Siam.—CARL MEZ (*idem* 232) has described a new Venezuelan genus (*Glomeropitcairnia*) of Bromeliaceae with two species.—J. C. ARTHUR (Annales Mycol. 3:18. 1905) has described a new genus (*Baeodromus*) of Uredineae with two species.—E. L. GREENE (Ottawa Nat. 18:215-216. 1905) has described new Canadian species of Malus and Fragaria (2).—W. FAWCETT and A. B. RENDLE (Trans. Linn. Soc. London II Bot. 7:1-13. pls. 1-2. 1904), in a monograph of the Jamaican species of Lepanthes (Orchidaceae), recognize 12 species, describing 5 as new.—N. L. BRITTON (Bull. N. Y. Bot. Garden 3:441-453. 1905), in his first "Contributions to the flora of the Bahama Islands," has published 15 new species and a new genus (*Bracea*) of Apocynaceae.—J. J. SMITH (Recueil Trav. Bot. Neerl. 1:49-51. pl. 2. 1904) has described a new genus (*Gynoglottis*) of Orchidaceae from Sumatra.—M. L. FERNALD (Rhodora 7:47-49. 1905) has described a new species of Comandra that ranges from Quebec to Assiniboia and Kansas.—F. STEPHANI (Hedwigia 44:74. 1905) has described two new Himalayan genera (*Gollaniella* and *Massalongoa*) of Hepaticae.—L. DIELS and E. PRITZEL (Bot. Jahrb. 35:564. 1905) have published a new Australian genus (*Pentaptilon*) of Goodeniaceae.—G. E. DAVENPORT (Fern Bulletin 13:18-21. 1905) has published a new Mexican Aneimia, with plates.—A. and E. S. GEPP (Jour. Botany 43:108. pl. 470. 1905) have described a new genus (*Leptosarca*) of the red algae from the South Orkneys.—J. M. C.

BERGE's second paper<sup>20</sup> on the formation of heterotypic chromosomes deals with the behavior of the chromatin from the telophase of the last division in the sporogenous tissue up to the strepsinema stage of the first mitosis in the microspore mother-cell. In a very early prophase of the first mitosis in the mother-cell, slender filaments are formed from the chromosomes of the sporogenous cell. Synapsis then takes place and at its close the filaments appear as the

<sup>20</sup> BERGHS, JULES, La formation des chromosomes hétérotypiques dans la sporogénèse végétale. II. Depuis la sporogonie jusqu'au spirème définitif dans la microsporogénèse de l'*Allium fistulosum*. La Cellule 21:383-397. pl. 1. 1904.



"thick spirem." During synapsis the dual nature of the filaments is evident. It is due to a longitudinal approximation of two filaments and leads to the formation of the thick spirem. The so-called longitudinal division is merely the reappearance of the line of approximation. Consequently the reduction in the number of chromosomes seen in the prophase of the heterotypic division is only an apparent reduction, due to the approximation of two somatic chromosomes, which in the mature chromosomes play the rôle of daughter chromosomes. The reduction is really accomplished by the first mitosis, which separates these daughter chromosomes.

The third paper<sup>21</sup> in the series deals with microsporogenesis in *Convallaria majalis*. The results confirm the conclusions already drawn from the author's study of *Allium fistulosum* and *Lilium speciosum*. The two daughter chromosomes which constitute the mature heterotypic chromosome represent two longitudinal parts of one segment of the thick spirem. This thick spirem is formed by the longitudinal approximation of slender chromatic filaments, two by two. This approximation takes place during the synaptic contraction, and the separation takes place in the strepsinema stage, resulting in an apparent longitudinal division. The heterotypic division is a reduction division, which distributes to the two poles complete somatic chromosomes.—C. J. CHAMBERLAIN.

THE RESEARCHES of SCHWARZ, ELFVING, VOCHTING, RACIBORSKI, and others on the influence of gravitation upon the rate of growth of erect and inverted organs have been extended by the investigations of HERING<sup>22</sup> carried on in PFEFFER's laboratory. This work adds support to the thesis generally maintained by earlier authors, that while the rate of growth of geotropic organs in natural position (vertical) is not affected by gravitation, such organs when inverted manifest a checking of the rate of growth in length. Improvement upon ELFVING's technique was secured by using artificial light of constant intensity instead of sunlight for keeping the organs parallel with gravitation; also by substituting a non-shrivelling substratum for bread crumbs for the growing of fungi. For such organs as could not be maintained in a vertical position by the use of light, recourse was taken to the use of pulleys and weights. The experimental material employed includes both positively and negatively geotropic organs as found in members of various genera of fungi, of monocotyledons, and of dicotyledons, as well as the branches of weeping trees. While nodes of grasses constitute an exception, the uniformity of behavior revealed by numerous other forms is so great as to permit a formulation of this general statement, namely, parallelotropic organs as a consequence of inversion suffer a reduction in the rate of growth in length. In the case of the sporangiophores of *Phycomyces* prolonged inversion is followed by

<sup>21</sup> BERGHS, JULES, La formation des chromosomes hétérotypiques dans la sporogénèse végétale. III. La microsporogénèse de *Convallaria majalis*. La Cellule 22:41-53. pl. I. 1904.

<sup>22</sup> HERING, GEORG, Untersuchungen über das Wachstum inversgestellter Pflanzengane. Jahrb. Wiss. Bot. 40:499-562. 1904.

accelerated growth, although a temporary inversion (one hour) is followed by diminished growth. In the case of the descending branches of weeping trees, gravitation not only causes a reduced rate of growth, but also determines the locus of origin of new shoots. Growth correlations similar to those observed by RACIBORSKI in tropical lianas were obtained.—RAYMOND H. POND.

LAWRENCE<sup>23</sup> has published a bulletin containing a summary of our present knowledge and the results of his own investigations of a serious apple disease found thus far only in Oregon and Washington, that was first described by CORDLEY<sup>24</sup> under the common name "apple tree anthracnose." The disease is also known under the following common names: Oregon canker, black canker, blackspot apple canker, blackspot, deadspot, and sour sap disease. The present writer proposes that the disease be known as the "blackspot canker." The fungus causing it was described by CORDLEY<sup>25</sup> under the name *Gloeosporium malicorticis*, and has been described also by PECK<sup>26</sup> under the name *Macrophoma curvispora*. This fungus is known to injure apple trees seriously in the Pacific northwest by the production of cankers upon the smaller twigs and branches. Similar cankers were produced by inoculation from apple cankers upon the cherry, plum, prune, and peach by LAWRENCE, and he is inclined to the belief that the same fungus is responsible for cankers upon all of the hosts named. As a rule cankers do not appear upon the larger branches and the trunk, owing apparently to the resistance offered by the corky outer layers of the bark of such regions to the penetration of the fungus. LAWRENCE here reports for the first time that the same fungus causes also a dry rot of stored apples that may be rather serious under certain conditions. The cankers may appear within a week from the time of infection; ordinarily appearing from November to February, rapidly completing their development after renewal of growth on the part of the host, and becoming mature by the next June or July. No definite statement can yet be made regarding either treatment of the disease or as to possible resistant varieties.—E. MEAD WILCOX.

A MUCH NEEDED INVESTIGATION of the rôle of latex in the metabolism of plants has been commenced by KNIEP,<sup>27</sup> and if continued may lead to valuable results. The paper here cited is presented in four sections. The introduction carefully reviews the literature, showing that theories are not supported by facts and that experimental results do not agree. The second section contains experi-

<sup>23</sup> LAWRENCE, W. H., Blackspot canker. Bull. Wash. Exp. Sta. 66. pp. 35. pls. 13. 1904.

<sup>24</sup> CORDLEY, A. B., Apple tree anthracnose: a new fungus disease. Bull. Oregon Exp. Sta. 60. pp. 3-8. pls. 1-3. 1900.

<sup>25</sup> CORDLEY, A. B., Some observations on apple tree anthracnose. BOT. GAZETTE 30:48-58. figs. 1-12. 1900.

<sup>26</sup> PECK, C. H., New species of fungus. Bull. Torr. Bot. Club 27:21. 1900.

<sup>27</sup> KNIEP, HANS, Ueber die Bedeutung des Milchsafte der Pflanzen. Flora 94:129-205. 1905.

mental evidence obtained by the author, which establishes that the latex participates very little, if at all, in the translocation of nutrient substances. Seedlings subjected to conditions intended to force an exhaustion of storage products showed no difference as to quantity or form of starch grains in the latex as compared with controls. The author does not regard the latex starch of the euphorbias with which he experimented as a typical storage product. SCHIMPER's results that the latex tubes of the euphorbias do not participate in the depletion of carbohydrates is verified. The third section comprises an anatomical study of thirty-six species distributed in seven families of laticiferous plants. DEBARY's view that latex tubes and sieve tubes are reciprocal tissues is rejected. The opinion of HABERLANDT that latex tubes function as translocation parenchyma is also discredited. The final section presents an ecological view of the problem, and two functions are assigned as ecological, namely, the closing of wounds by the exudation of latex, and protection against animals secured by presence of poisonous, acrid, or ill-smelling substances. That the problem remains unsolved, and that the chief value of his paper consists in formulating the present status of investigation as well as in indicating promising lines of research, is fully realized by the author.—RAYMOND H. POND.

MITOSIS in the salamander (*Salamandra maculata*) has been investigated by KOWALSKI<sup>28</sup> under the direction of GREGOIRE. The object of the investigation was to compare typical animal mitoses with the mitoses in the roots of *Trillium* as described by GREGOIRE and WYGAERTS (see BOT. GAZETTE 38:396. 1904). Mitosis was studied in various tissues, but principally in the epithelial cells. In general it may be said that even in minute details the structures and the sequence of events are essentially the same as in *Trillium*. In the telophase the action of the nuclear sap outside the chromosome results in the production of anastomoses between the neighboring chromosomes and between parts of the same chromosome; while the action of the sap within the chromosome brings about an alveolar and reticular structure. Each chromosome forms a network of lamellae and filaments of various shapes and sizes which cross each other in every direction. The entire chromatic network of the nucleus is made up of the individual networks. The behavior of the chromatin in the prophase is strong evidence in favor of the individuality of the chromosome. The longitudinal splitting of the chromosome is not due to the bipartition of a series of chromatic disks imbedded in a substratum, but consists simply in the longitudinal cleavage of a chromatic ribbon. No disk spirum is formed at the telophase, nor is any spirem formed at the prophase. The nuclear membrane is formed by the condensation of the cytoplasm bordering upon the nuclear vacuole, and at its formation no cytoplasm is included within the nuclear cavity.—C. J. CHAMBERLAIN.

<sup>28</sup> KOWALSKI, J., Reconstitution du noyau et formation des chromosomes dans les cinèses somatiques de la larve de Salamandre. La Cellule 21:349-377. pls. 1-2 1904.

SEVERAL RECENT INVESTIGATIONS have brought to light a curious condition in certain plankton diatoms which is believed to be a method of spore formation. The contents of certain cells break up into a number of small bodies which are termed "microspores." These structures have been recently investigated by KARSTEN<sup>29</sup> in a species of *Corethron*. Their development begins in this form with a remarkable increase in the number of nuclei in a single diatom, until as many as 128 are present. The nuclei divide mitotically and the protoplasm successively until this large number of bodies are found, which however often remain connected with one another by delicate fibrils of protoplasm. KARSTEN believes that "microspores" which escape from the mother diatom are gametes and unite with one another in pairs to form a zygospore. Further, there is evidence that the zygospore gives rise to two new diatoms and that each of these contains at first two nuclei, one of which afterwards breaks down. If this should be established, we should have presented in the diatoms a method of sexual reproduction followed by a type of germination with two successive mitoses apparently of the same character as in the desmids. It is fair to say, however, that KARSTEN seems to draw his conclusions from a rather imperfect series of stages.—B. M. DAVIS.

PELETRISOT<sup>30</sup> has published an extended study of the development of the seeds of Ericaceae, including in his examination twenty-six genera and sixty-two species. Such a survey can only mean a glimpse of a general situation, which subsequent research will develop properly. Aside from anatomical details of tissues, which can hardly be related as yet, the general morphological situation seems to be about as follows. The most striking feature of the embryo sac is the development of a large haustorial pouch at each end. This haustorium varies much in size in different genera, reaching its maximum in *Arbutus*; and also in its degree of separation from the central cavity, sometimes being separated only by a slight constriction, and in other cases by a narrow, more or less prolonged neck. In many of the genera there is also a well-developed jacket-layer investing the central cavity of the sac. The synergids are often beaked and extended into the micropyle, and the antipodals are ephemeral.

Aside from the extent of the survey and the prolix presentation, the most notable feature of the paper is the absence of all knowledge of any English or American publications dealing with similar haustorial developments.—J. M. C.

THE POSITION of the monocotyledons is discussed in a recent paper by FRITSCH.<sup>31</sup> Since the geological history is so fragmentary, we must rely upon the evidence of comparative morphology. After discussing this evidence,

<sup>29</sup> KARSTEN, G., Die sogenannten "Mikrosporen" der Plankton-Diatomeen und ihre weitere Entwicklung beobachtet an *Corethron Valdiviae*. Ber. Deutsch. Bot. Gesells. 22:544-554. pl. 23. 1904.

<sup>30</sup> PELETRISOT, C.-N., Développement et structure de la graine chez les Ericacées. Jour. Botanique 18:309-367, 386-402. figs. 173. 1904.

<sup>31</sup> FRITSCH, K., Die Stellung der Monokotylen im Pflanzensystem. Engler's Bot. Jahrb. Beiblatt No. 79. pp. 22-40. 1905.

including recent investigations in anatomy, the conclusion is reached that the Ranales and Helobiales are related groups; not, however, that any particular family in one has come from a family in the other, but that both have been differentiated from a common ancestry. HALLIER's theory that the entire group of the angiosperms is monophyletic and that it has come from a Ranales-like type, is, according to FRITSCH, a broader conclusion than is warranted by the present condition of our knowledge. Since the dicotyledons show some characters more nearly resembling conditions found in gymnosperms, the dicotyledons should be placed before the monocotyledons in any scheme of classification.—C. J. CHAMBERLAIN.

SHIBATA<sup>32</sup> has investigated the chemotaxis of the sperms of *Isoetes*. He finds the stimulation limit to be  $m/20000$  malic acid. Of seventy other substances tested in concentrations of  $m/10$  to  $M/100$ , only neutral salts of succinic, fumaric, and *d*-tartaric acids, which are in structure closely allied to malic acid, were attractive, the lower limit being  $m/100$  to  $5m/1000$ . WEBER's law was found applicable. The relative chemotactic effect of H-ions was found equal in various mineral acids and salts; similarly, OH-ions from equivalent solutions of alkalies acted alike. Other interesting results bear on negative chemotaxis of anions, osmotaxis, and the nature of the reactions. The notice is a preliminary one.—C. R. B.

KOERNICKE<sup>33</sup> has reviewed several recent cytological papers, thus bringing his work on "The present condition of cell studies" up to date. The only important change of opinion noted is in regard to the occurrence of a reduction division in plants. The evidence given in the previous paper was against such a division, but in light of the more recent researches, especially those of FARMER and MOORE, KOERNICKE believes that the evidence in favor of reduction division is gradually increasing. The work of WILLIAMS, GREGORY, LOTSY, ROSENBERG, BOVERI, GRÉGOIRE and WYGAERTS, and HÄCKER are considered in this summary.—CHARLES J. CHAMBERLAIN.

WIESNER,<sup>34</sup> who has already pointed out two cases of the dropping of leaves which he calls *Sommerlaubfall* and *Treiblaubfall*, adds another, due to high temperature combined with drouth, which he calls *Hitzelaubfall*. The death of the leaves is due to excessive transpiration not covered by the available water. Naturally the peripheral leaves and especially those reached most directly by the sun are most affected. Observations are adduced from the author's extended tour in the United States during the months of August and September.—C. R. B.

<sup>32</sup> SHIBATA, K., Studien über die Chemotaxis von *Isoetes*-Spermatozoiden. Ber. Deutsch. Bot. Gesells. 22:478-484. 1904.

<sup>33</sup> KOERNICKE, M., Die neueren Arbeiten über die Chromosomreduktion im Pflanzenreich und daran anschliessende karyokinetische Probleme. Bot. Zeitung 62:305-314. 1904.

<sup>34</sup> WIESNER, J., Ueber den Hitzelaubfall. Ber. Deutsch. Bot. Gesells. 22:501-505. 1904.

STEMS OF CALAMITES with attached roots are rare, but several specimens have been described by MASLEN,<sup>35</sup> whose account clears up several doubtful points. The roots in question are mainly adventitious and spring from the nodes of the aerial as well as the subterranean stems. These roots may be distinguished from branches among other ways by their point of origin, which however is different from that of the roots of Equisetum. The writer finds no evidence for connecting the roots with the infranodal organs described by WILLIAMSON.—M. A. CHRYSLER.

GUIGNARD<sup>36</sup> has presented further interesting details in connection with double fertilization in the Malvaceae, using *Althaea rosea* and *Hibiscus Trionum*. Each large and very characteristic pollen grain puts out several pollen tubes, which advance through the tissues of the style and the nucellus in a peculiar way. In *Hibiscus*, when the embryo sac is reached, the tube branches irregularly. The formation of the generative nucleus and male cells, and the occurrence of starch are described in detail.—J. M. C.

MISS SARGANT and Miss ROBERTSON<sup>37</sup> call attention to the fact that the furrows on the dorsal face of the scutellum in *Zea Mais* should be regarded as glands which increase the extent of secreting surface. These glands are situated in contact with the floury part of the endosperm, and so secure a rapid transfer of food to the seedling while it as yet has no assimilating organs. An interesting observation is the presence of amphivasal strands and of transfusion tissue in the scutellum.—M. A. CHRYSLER.

DRABBLE's studies on the roots of palms<sup>38</sup> show that the polystelic condition found in *Areca* is not exceptional, but that it commonly occurs in the proximal region of secondary roots. These separate steles usually fuse in the distal region of the root to form a single cylinder; certain vascular strands, however, may remain unfused and constitute the well-known medullary strands. The monostelic central cylinder of palm roots has thus by no means a simple origin.—M. A. CHRYSLER.

WALLER finds<sup>39</sup> that practically no sea plants give blaze currents following an induction shock, while practically no land plants fail to do so. Resistance of young tissues is very high, and is lowered much by one shock, which

<sup>35</sup> MASLEN, A. J., The relation of root to stem in Calamites. Ann. Botany 19: 61-74. pls. 1-2. 1905.

<sup>36</sup> GUIGNARD, L., La double fécondation chez les Malvacées. Jour. Botanique 18: 296-308. figs. 16. 1904.

<sup>37</sup> SARGANT, E., and ROBERTSON, A., The anatomy of the scutellum in *Zea Mais*. Ann. Botany 19: 115-124. pl. 5. 1905.

<sup>38</sup> DRABBLE, ERIC, On the anatomy of the roots of palms. Trans. Linn. Soc. London. II. Bot. 6: 427-490. pls. 48-51. 1904.

<sup>39</sup> WALLER, A. D., On the blaze currents of vegetable tissues. Jour. Linn. Soc. Bot. 37: 32-50. 1904.

probably means that the lacking electrolytes are produced by dissociation upon passing the induction current. Killed tissues show no blaze currents.—C. R. B.

TREBOUX<sup>40</sup> in a preliminary paper announces that for chlorophyllous plants the source of N *par excellence* is the ammonia radicle, rather than amido-acids. The significance whereof lies in its relation to a general theory of proteid synthesis to which the author has been led by his experiments.—C. R. B.

VON SPIESS shows<sup>41</sup> that the so-called green aleurone does not exist, such grains being really more or less degenerate chloroplasts. Bluish aleurone grains occur in maize, the color being due to anthocyan.—C. R. B.

GATIN<sup>42</sup> has described cases of polyembryony in two palms, *Phoenix canariensis* and *Pinanga patula*, but gives no account of the origin of the embryos.—J. M. C.

BONNIER<sup>43</sup> has compared in detail the embryo sac of gymnosperms and angiosperms, reaching the conclusion that the most fundamental difference between the two groups is that in gymnosperms all the eggs formed in an embryo sac are alike; while in angiosperms the two eggs usually produced are unlike, one forming the embryo, the development from the other stopping at the proembryo stage (endosperm). This is an effort to include double fertilization in contrasting gymnosperms and angiosperms, but does not explain anything.—J. M. C.

MISS RIDDLE<sup>44</sup> has studied the development of *Staphylea trifoliata* from the megasporangiate archesporial cell of the embryo. The account presents no unusual features, but it is a matter of interest to note that double fertilization was observed. A definite account of some of the forms of Sapindales was much needed.—J. M. C.

<sup>40</sup> TREBOUX, O., Zur Stickstoff-Ernährung der grünen Pflanzen. Ber. Deutsch. Bot. Gesells. 22:570-572. 1905.

<sup>41</sup> VON SPIESS, KARL, Ueber die Farbstoffe des Aleurone. Oesterr. Bot. Zeits. 54:440-446. 1904.

<sup>42</sup> GATIN, C. L., Quelques cas de polyembryonie chez plusieurs espèces de palmiers. Rev. Gén. Botanique 17:60-65. 1905.

<sup>43</sup> BONNIER, GASTON, Remarques sur la comparaison entre les angiospermes et les gymnospermes. Rev. Gén. Botanique 17:97-108. figs. 6. 1905.

<sup>44</sup> RIDDLE LUMINA C., Development of the embryo sac and embryo of *Staphylea trifoliata*. Ohio Naturalist 5: 320-325. pls. 19-20. 1905.

## NEWS.

PROFESSOR F. W. OLIVER, University College, London, has been elected a Fellow of the Royal Society.

DR. E. PFITZER, University of Heidelberg, has been elected associate member of the Royal Botanical Society of Belgium.

ALFRED ERNST, professor of botany at Zürich, has received from the government \$1000 for botanical studies at Buitenzorg.

DR. GEORGE BITTER, docent in botany at Münster, has been appointed director of the Botanical Garden at Bremen.—*Science*.

PROFESSOR HUGO DEVRIES, University of Amsterdam, has been elected associate member of the Royal Academy of Belgium.

W. A. KELLERMAN has returned from a three months' exploration of Guatemala with a large amount of material, especially parasitic fungi.

PROFESSOR E. C. JEFFREY, Harvard University, has received a grant of \$200 from the Elizabeth Thompson Science Fund "for the study of cupressineous conifers."

A. S. HITCHCOCK, U. S. Department of Agriculture, has been transferred to the Office of Botanical Investigations and Experiments, his position being styled "systematic agrostologist."

PROFESSOR THEOPHILE DURAND, director of the Botanical Garden at Brussels, and Professor JEAN MASSART, University of Brussels, have been elected corresponding members of the Royal Academy of Belgium.

F. E. LLOYD, Teachers College, Columbia University, has received a grant of \$500 from the Carnegie Institution to aid him in continuing his studies on stomatal action and transpiration in desert plants. He spends three months at the Desert Botanical Laboratory for this purpose.—*Science*.

IT IS ANNOUNCED by *Science* that Professor DOUGLAS H. CAMPBELL will spend next year in an extensive trip through Europe, Africa, and Asia. He will visit the regions about Victoria and Zambesi Falls; the botanical gardens at Paradeniya and Buitenzorg; and will then return by way of the Philippine Islands.



# BOTANICAL GAZETTE

*JUNE, 1905*

## LEGUMINOUS RUSTS FROM MEXICO.

J. C. ARTHUR.

THE following thirty-seven species of Uredinales, represented by 128 numbered collections, are, with two exceptions, part of the rich fruits of three vacation trips into Mexico, made by Mr. E. W. D. HOLWAY in 1898, 1899, and 1903. Some of the material secured on these excursions has already been reported upon by Mr. HOLWAY in an article in this journal (31:326-338. 1901), which included descriptions of thirty-one new species; a still earlier trip, made in 1896, was also reported by Mr. HOLWAY in this journal (24:23-38. 1897), in which forty-five new species of Uredineae were described, the descriptions being drawn by Dr. P. DIETEL, and with two species of ascomycetous fungi, one being the type of a new genus. Much material remains to be studied, which will undoubtedly yield many more new species.

The amount of excellent material secured by Mr. HOLWAY within the limited periods at his command shows him to be a collector of unusual activity and acumen. His specimens are ample, and as a rule contain the various spore stages, or all that could reasonably be expected to occur at one season of the year. Another most commendable feature in making these collections is the care taken to secure the exact determination of the host whenever feasible. Not only are bits of the inflorescence and fruit included, but whenever the host is in any way unfamiliar, specimens suitable for the phanerogamic herbarium are taken illustrating the foliage, flowers, and fruit of the plants as well as possible. These are given the same numbers as used for the fungi found on them. They are subsequently sent to specialists for determination, by which means accuracy of naming

is insured; incidentally also the leading herbaria of the country have been enriched with many valuable specimens, while not a few new species of flowering plants have been brought to light.

The collections made by Mr. HOLWAY show that Mexico has an abundant rust flora, and especially so in the groups represented by the genera *Ravenelia* and *Uropyxis*. If collections made during September, October, and November, and over a comparatively small part of that great country have proved so interesting and valuable, more extended search is likely to be rewarded with almost or quite equal results for some time to come.

The following enumeration includes the portion of Mr. HOLWAY'S uredineous collections in Mexico, not heretofore published, possessing leguminous hosts, *i. e.*, the rusts occurring upon members of the families Fabaceae, Cassiaceae, and Mimosaceae.

1. *UROMYCES TRIFOLII* (A. & S.) Lev.—On *Trifolium amabile* HBK., Jalapa, Oct. 3, 1898, no. 3091: *Trifolium* sp., Pachuca, Oct. 27, 1903, no. 5245; City of Mexico, Oct. 28, 1899, no. 3746.

2. *UROMYCES MEDICAGINIS-FALCATAE* Wint.—On *Medicago denticulata* Willd., Toluca, Sept. 19, 1898, no. 3129.

3. *Uromyces rugosa*, n. sp.—Uredosori hypophyllous, cinnamon-brown; uredospores globose, 20–24 by 21–27 $\mu$ ; wall light yellow, medium thick, 2–2.5 $\mu$ , minutely and sparsely verrucose, pores 8, scattered: teleutosori hypophyllous, small, round, 1<sup>mm</sup> or less across, scattered or somewhat gregarious, soon naked, pulverulent, dull chocolate-brown; teleutospores broadly oval or globose, 18–22 by 21–27 $\mu$ , wall dark chestnut-brown, medium thick, 2–3 $\mu$ , rugose or irregularly and closely verrucose, apex usually bearing a very low, hyaline umbo; pedicel colorless, short, fragile, mostly deciduous.—On *Lupinus* sp., Amecameca, Oct. 21, 1903, no. 5208.

The very rough and opaque spores easily separate this species from all others reported from North America on *Lupinus*. The uredo stage was not well shown on the specimens studied, and is consequently incompletely described.

4. *Uromyces montanus*, n. sp.—Teleutosori hypophyllous, small, round, crowded in circinating groups, 5–10<sup>mm</sup> across, centripetal in development, early naked, cinnamon-brown or darker, usually cinereous from germination; teleutospores oval or obovate, pale, 18–24 by 30–40 $\mu$ , wall very pale brownish, smooth, thin, 1–1.5 $\mu$ ,

thickened at apex,  $5-7\mu$ , pedicel colorless, thick, as long as the spore or shorter.—On *Lupinus mexicanus* HBK., Nevada de Toluca, 10,400<sup>ft</sup> alt., Oct. 16, 1903.

This collection also showed well-developed aecidia of *Uromyces Lupini* B. & C. upon the same leaves. The teleutospores germinate in the sorus upon maturity.

5. *UROMYCES LUPINI* B. & C.—On *Lupinus elegans* HBK., Toluca, Sept. 19, 1898, no. 3177; *Lupinus* sp., Pachuca, Oct. 5, 1899, no. 3575; Zapotlan, Oct. 9, 1903, no. 5140; Nevada de Toluca, Oct. 15, 1903, no. 5154; Amecameca, Oct. 21, 1903, no. 5209.

6. *Uromyces Cologaniae*, n. sp.—Uredosori hypophyllous, scattered, round, small,  $0.25^{\text{mm}}$  or less across, soon naked, pulverulent, pale cinnamon-brown, ruptured epidermis barely noticeable; uredospores globose,  $16-23$  by  $20-27\mu$ , wall pale cinnamon-brown, thin,  $1.5-2\mu$ , evenly and minutely echinulate, pores 3-4, equatorial: teleutospori hypophyllous, scattered, round, small,  $0.25^{\text{mm}}$  across, soon naked, pulverulent, cinnamon-brown, ruptured epidermis barely noticeable; teleutospores oval or globose,  $16-20$  by  $18-26\mu$ , rounded at both ends, wall cinnamon-brown, thin,  $1.5-2\mu$ , closely and finely verrucose, apex a little thicker or with a very low, pale umbo,  $2-4\mu$ ; pedicel colorless, short, fragile; mostly deciduous.—On *Cologania pulchella* HBK., Patzcuaro, Oct. 20, 1898, no. 3192 (type); Toluca, Sept. 20, 1898, no. 3179; Uruapam, Oct. 11, 1899, no. 3615; *C. congesta* Rose, Toluca, Sept. 20, 1898, no. 3179; *C. affinis* Mart. & Gal., Jalapa, Oct. 3, 1898, no. 3193; *Cologania* sp., Oaxaca, Oct. 21, 1899, no. 3703.

The determination of the several hosts was made by Dr. J. N. ROSE of the U. S. National Museum, all with some slight question, as the material was far from complete.

7. *UROMYCES APPENDICULATUS* (Pers.) Unger.—On *Phaseolus vulgaris* L., City of Mexico, Oct. 15, 1898, no. 3049; Atequiza, State of Jalisco, Oct. 6, 1903, no. 5120; *P. retusus* Benth., near Tula, Sept. 20, 1898, no. 3161; *P. anisotrichus* Scheele, Rio Hondo, near City of Mexico, Sept. 22, 1898, no. 3155; *P. disophyllus* Benth., Chapala, Sept. 18, 1899, no. 3455; *P. coccineus* Jacq., City of Mexico, Oct. 9, 1898, no. 3037; Dos Rios, near City of Mexico, Sept. 22, 1898, no. 3094; Uruapam, Oct. 12, 1899, no. 3625; *P. obvallatus* Scheele, Santa Fé, near City of Mexico, Oct. 18, 1903, no. 5170;

Amecameca, Oct. 20, 1903, no. 5188: *P. atropurpureus* Moc., Iguala, State of Guerrero, Nov. 4, 1903: *Phaseolus* sp., Cuernavaca, Sept. 24, 1898, no. 3021; Cuautla, Oct. 12, 1898, no. 3070, and Oct. 22, 1903, no. 5217; near Tula, Sept. 21, 1898, no. 3187; Etlá, State of Oaxaca, Oct. 23, 1899, no. 3729; Guadalajara, Sept. 22, 1903, no. 5021, Iguala; Nov. 4, 1903, no. 5336.

The Mexican collections of this species of rust do not vary in any noticeable way from those made in the United States. *Uromyces obscurus* D. & H. was founded on a *Phaseolus* rust having what was taken to be a peculiar form of *Aecidium*, but which proves to be a species of *Synchytrium*. This name is therefore a synonym of *U. appendiculatus*.

8. *UROMYCES FABAE* (Pers.) DeB.—On *Faba vulgaris* L., Toluca, Sept. 17, 1898, no. 3189; Patzcuaro, Oct. 13, 1899, no. 3628; and Oaxaca, Oct. 24, 1899, no. 3733.

9. *UROMYCES TENUISTIPES* D. & H.—On *Meibomia* sp., Dos Rios, near City of Mexico, Sept. 22, 1898, no. 3095; Toluca, Sept. 19, 1898, no. 3097; Cardenas, Oct. 22, 1898, no. 3148; Atequiza, State of Jalisco, Sept. 26, 1899, no. 3503.

The teleutospores are minutely rugose, although they appear smooth when wet. The apex of the spore has a very low, semihyaline umbo, which often disappears, leaving a shallow depression, as mentioned in the original description (BOT. GAZ. 24:25. 1897).

10. *UROMYCES MEXICANUS* D. & H.—On *Meibomia* sp., Cuernavaca, Sept. 24, 1898, no. 3019, and Sept. 28, 1898, no. 3124; near Tula, State of Hidalgo, Sept. 21, 1898, no. 3195; Cardenas, State of San Luis Potosi, Oct. 22, 1898, no. 3150; Rio Hondo, near City of Mexico, Sept. 22, 1898, no. 3154; Chapala, Sept. 18, 1899, no. 3447.

11. *UROMYCES HEDYSARI-PANICULATI* (Schw.) Farl.—On *Meibomia amplifolia* (Hemsl.) Kuntze, Patzcuaro, Oct. 20, 1898, no. 3141: *M. elegans* (Desv.) Kuntze, Rio Hondo, near City of Mexico, Oct. 4, 1899, no. 3569: *M. strobilacea* (Schl.) Kuntze, Guadalajara, Oct. 12, 1903, no. 5146: *Meibomia* sp., City of Mexico, Oct. 14, 1898, no. 3048; Cuernavaca, Sept. 29, 1899, no. 3518 with uredospores only; Morelia, Oct. 14, 1899, no. 3633; Oaxaca, Oct. 18, 1899, nos. 3658, 3659, Oct. 23, 1899, nos. 3716, 3723, Nov. 11, 1903, no. 5385; Santa Fé, near City of Mexico, Oct. 18, 1903, no. 5165; Tlalpam, near City of Mexico, Oct. 19, 1903, no. 5180.

12. **Uromyces Clitoriae**, n. sp.—Uredosori hypophyllous; uredospores globoid, about  $23-27\mu$  in diameter, wall thick,  $3\mu$ , fuscous, evenly and sparsely echinulate, pores apparently 2: teleutosori hypophyllous, small, round, scattered, dark cinnamon-brown, soon naked; teleutospores ellipsoid,  $20-24$  by  $22-30\mu$ , wall chestnut-brown, evenly thick,  $3-3.5\mu$ , minutely and evenly verrucose; pedicel delicate, colorless, less than the length of the spore, caducous.—On *Clitoria mexicana* Link, Jalapa, Oct. 5, 1898, no. 3088.

Only a few uredospores were seen, which were found in parasitized sori. The sculpturing of the teleutospores is minute but very distinctly shown when dry.

13. **Uromyces bauhiniicola**, n. sp.—Spermogonia epiphyllous, gregarious, punctiform, fuscous, subepidermal, seen in section globose,  $60-130\mu$  in diameter: teleutosori at first hypophyllous, becoming amphigenous, small, round, about  $1\text{mm}$  in diameter, often confluent, early naked, blackish; teleutospores broadly oval or globoid,  $15-21$  by  $20-24\mu$ ; wall dark chestnut-brown, semi-opaque, thick,  $2.5-3.5\mu$ , prominently rugose, thicker and paler at apex,  $5-7\mu$ ; pedicel colorless, firm, as long as the spore.—On *Bauhinia Pringlei* Wats., Guadalajara, Sept. 28, 1903, no. 5060 (type): *Bauhinia* sp., Iguala, Nov. 4, 1903, no. 5334.

Readily distinguished from the four or five species occurring upon *Bauhinia* in South America by the very dark, rugose spores, unaccompanied by uredospores. The spores germinate somewhat readily in the sori, not long after maturity.

14. **PHRAGMOPYXIS DEGLUBENS** (B. & C.) Diet.—On *Brittonamra Edwardsii* (A. Gr.) Kuntze (*Cracca Edwardsii* A. Gray), Cuernavaca, Oct. 30, 1903, no. 5278.

This is the first time the host of this rare and interesting species has been definitely determined. It has only twice been reported before, once in Ecuador on an undetermined species of *Coursetia*, a genus closely related to *Brittonamra*. The type collection is recorded on "leaves of some leguminous plant," and is said to come from Texas (Grev. 3:55), which latter, however, must be an error. The specimen in the cryptogamic herbarium of Harvard University says, "Northern Sonora," and bears the collector's number, the same as recorded by BERKELEY in *Grevillea*. A specimen in the herbarium of the Department of Agriculture at Washington, D. C., says "N. Mexico," but does not bear the collector's number. Both of these specimens are undoubtedly part of the one original collection made by C. Wright. The Washington specimen consists of two leaflets, 5 by  $12\text{mm}$ ,

elliptical, entire, nearly smooth above, slightly hirsute below with scattered hairs, mucronate, short petioluled, texture firm, bearing a few, well-formed, amphigenous teleutosori. The specimen was compared, under the guidance of Dr. J. N. ROSE, with specimens in the phanerogamic herbarium of the U. S. National Museum, but could not be matched.

The collection by Mr. HOLWAY is furthermore noteworthy in possessing aecidia, not heretofore known, which are rather pale and inconspicuous. They may be described as follows: Aecidia hypophyllous, or somewhat amphigenous, crowded in small groups, pale yellow, without peridium, but sparingly encircled by incurved paraphyses; aecidiospores catenulate, globose or globose-oblong, 13-17 by 15-19 $\mu$ , wall very pale yellow, thin, 1 $\mu$ , finely and closely verrucose, paraphyses small, cylindrical, 5-7 by 24-30 $\mu$ , more or less contorted, wall usually thick, sometimes nearly obliterating the lumen, smooth, colorless: spermogonia epiphyllous, few in groups opposite the aecidia, brownish-yellow, punctiform, inconspicuous, subcuticular, conical, small, 60-80 $\mu$  broad and half as high, ostiolar filaments 20-24 $\mu$  long, free.

**CALLIOSPORA**, nov. gen.—Teleutosori arising from beneath the epidermis, soon naked; teleutospores 2-celled by transverse partition, wall colored, with an external layer which swells in water, germ pores 2 in each cell, latéral. Aecidium and uredo wanting. Spermogonia arising from beneath the cuticle, conical.

15. **Calliospora Holwayi**, n. sp.—Spermogonia epiphyllous, numerous over areas 2-7<sup>mm</sup> across, punctiform, golden yellow, becoming brown, subcuticular, conical, 80-125 $\mu$  broad: teleutosori epiphyllous, scattered, sometimes confluent, small, round, blackish-brown; teleutospores elliptical, 26-34 by 40-51 $\mu$ , rounded at both ends, slightly or not constricted at the septum, inner wall chocolate-brown, thick, 3-4 $\mu$ , pores two in each cell, outer wall colorless, 2-3 $\mu$  thick in water, smooth; pedicel colorless, as long as the spore, swelling in water to the diameter of the spore and bursting.—On *Eysenhardtia amorphoides* HBK., Guadalajara, Sept. 28, 1903, no. 5059 (type), Sept. 29, 1903, no. 5068; Oaxaca, Oct. 25, 1899, no. 3737: *E. orthocarpa* Wats., Etlá, State of Oaxaca, Nov. 13, 1903, nos. 5404 and 5405.

This species resembles *Uropyxis Eysenhardtiae* (D. & H.) Magn., but differs not only in the absence of the uredo, but in the position of the sori, the measurements of the teleutospores, and their smooth, colorless, outer wall. The collections have been examined by Dr. J. N. ROSE, who says that the species of *Eysenhardtia* have not been sufficiently studied, and some doubt must attach to the determination of the several numbers.

16. *Calliospora Farlowii*, n. sp.—Spermogonia caulicolous, and sparingly on midrib of leaf, small, punctiform, yellowish-brown, conical,  $80-100\mu$  broad, ostiolar filaments  $25-40\mu$  long: teleutosori caulicolous, large, confluent, early naked, pulverulent, cinnamon-brown; teleutospores elliptical,  $18-24$  by  $29-42\mu$ , rounded at both ends, slightly or not constricted at the septum, inner wall cinnamon-brown,  $2-3\mu$  thick, pores 2 in each cell, outer wall colorless, barely noticeable when swollen in water, minutely verrucose; pedicel colorless, about  $6\mu$  thick, short and mostly deciduous.—On *Parosela domingensis* (DC.) Heller (*Dalea domingensis* DC.), Orizaba, Feb., 1888 (W. G. Farlow).

I am indebted to the collector for excellent material of this interesting species. In the selection of the specific name I take the opportunity of showing my appreciation of courtesies in sending me material, and also my high regard for the eminent services rendered by Dr. FARLOW to botanical science.

17. *Calliospora Diphysae*, n. sp.—Spermogonia amphigenous, crowded in dendritic groups, or disposed in lines, pale brown, bullate or hemispherical, subcuticular,  $100-175\mu$  broad and less than half as high: teleutosori amphigenous and caulicolous, round or elongated,  $1-5^{mm}$  long, early naked, nearly black; teleutospores elliptical,  $30-33$  by  $45-50\mu$ , rounded at both ends, not constricted at septum, inner wall dark chestnut-brown,  $3-4\mu$  thick, pores 2 in each cell, outer gelatinous, pale amber-color,  $3-4\mu$  thick in water, sparsely and evenly verrucose; pedicel half length of spore or longer, colorless, firm above, at base slightly bulbous and swelling in water to bursting.—On *Diphysa suberosa* Wats., Rio Blanco, near Guadalajara, Sept. 30, 1903, no. 5082.

18. UROPYXIS NISSOLIAE (D. & H.) Magn.—On *Nissolia laxior* Rose, Guadalajara, Sept. 25, 1903, no. 5039: *N. hirsuta* DC., Sayula, State of Jalisco, Oct. 8, 1903, no. 5127; Cuautla, State of Morelos, Oct. 23, 1903, no. 5230: *Nissolia* sp., Cuernavaca, Nov. 1, 1903, no. 5309.

These collections, except the one made in November, show a few uredospores among the teleutospores. The uredospores are globoid or ellipsoid, pale yellow or nearly colorless,  $12-16\mu$  in diameter, wall very thin,  $0.75\mu$ , finely verrucose, pores very indistinct, few. The paraphyses seen are capitate, thin-walled, and colorless.

19. *UROPYXIS DALEAE* (D. & H.) Magn.—On *Parosela Dalea* (L.) Britt. (*Dalea alopecuroides* Willd.), Guadalajara, Sept. 26, 1903, no. 5048; *P. mutabilis* (Willd.) Rose, Toluca, Sept. 19, 1898, no. 3188; Amecameca, Oct. 20, 1903, no. 5196, Nov. 20, 1903, no. 5426; *P. acutifolia* (DC.) Rose, Cuautla, State of Morelos, Oct. 23, 1903, no. 5227; *P. Holwayi* Rose, Iguala, State of Guerrero, Nov. 3, 1903, no. 5319; *P. trijoliata* Rose, near Tacubaya, City of Mexico, Oct. 7, 1896, without number; Aguascalientes, Oct. 9, 1903, no. 7705 (*Rose & Painter*).

20. *Uredo Æschynomenis*, n. sp.—Sori mostly hypophyllous, grouped on small reddish spots, or scattered, subepidermal, small, globose, with pseudoperidium formed of imbricated paraphyses by the union of the slender stipes, the free capitate ends lining the inner wall, dehiscent by a central orifice; uredospores stylate, broadly elliptical or globoid, 14–18 by 16–23 $\mu$ , wall pale yellow, thin, 1 $\mu$ , very minutely verrucose, pores obscure, about 6, scattered.—On *Æschynomene americana* L., Cuautla, State of Morelos, Oct. 22, 1903, no. 5220.

The spores of this collection are much like those of *Uropyxis Nissoliae*, the hosts of the two species being closely related. But no genus of leguminous rusts known to the writer contains species with a pseudoperidium for the uredo. Until the teleutospores are discovered, it will be impossible to state the affinities of the species.

21. *Ravenelia Lysilomae*, n. sp.—Spermogonia epiphyllous, crowded in small groups, punctiform, rather large, pale brownish-yellow, subcuticular, flattened hemispherical, 80–130 $\mu$  wide, one-fourth as high: teleutostori epiphyllous on pale spots, becoming amphigenous, small, 0.25–0.5<sup>mm</sup> across, chestnut-brown, subepidermal, numerous hyphoid paraphyses intermixed with the spores, inconspicuous; teleutospore-heads chestnut-brown, 7–9 cells across, 80–120 $\mu$  in diameter, smooth, cysts appressed beneath the head, extending from periphery to pedicel, united laterally; pedicel colorless, short, deciduous; paraphyses cylindrical, 7–10 by 30–40 $\mu$ , light golden-brown, wall thin or rarely thick.—On *Lysiloma tergemina* Benth., Iguala, State of Guerrero, Nov. 3, 1903, no. 5317.

22. *RAVENELIA VERRUCOSA* Cke. & Ell.—On *Leucaena microphylla* Benth., Iguala, State of Guerrero, Nov. 3, 1903, no. 5314.



This collection differs slightly from the type in having heads almost or quite smooth, and with paraphyses fewer and paler.

23. *RAVENELIA LEUCAENAE* Long.—On *Leucaena diversifolia* Benth., Etlá, State of Oaxaca, Nov. 13, 1903, no. 5408: *L. esculenta* DC., Etlá, State of Oaxaca, Nov. 13, 1903, no. 5413; Iguala, State of Guerrero, Nov. 3, 1903, no. 5311: *Leucaena* sp., Guadalajara, Sept. 25, 1903, no. 5044; and Tehuacan, State of Puebla, Nov. 7, 1903, no. 5349.

There appears to be considerable uncertainty in the exact determination of the species of *Leucaena*. Although these numbers have been submitted to competent authorities, the correctness of the specific names employed here cannot be vouched for.

24. *RAVENELIA EXPANSA* Diet. & Holw.—On *Acacia fliculoides* (Cav.) Trel. (*A. flicina* Willd.), Iguala, State of Guerrero, Nov. 3, 1903, no. 5312: *A. cochliacantha* Humb. & Bonp., Iguala, State of Guerrero, Nov. 3, 1903, no. 5315; Tehuacan, State of Puebla, Nov. 8, 1903, no. 5353: *Acacia* sp., Yautepec, Oct. 24, 1903, no. 5237.

25. *RAVENELIA SILIQUAE* Long.—On *Acacia pennatula* Benth., Etlá, State of Oaxaca, Nov. 14, 1903, no. 5395.

The type was seen by Mr. LONG only on the fruit, but the present collection, which does not differ in any perceptible way from the type, only shows rust on the leaves. No teleutospores could be found.

26. *Ravenelia gracilis*, n. sp.—Spermogonia amphigenous, punctiform, crowded in groups, prominent, subcuticular, hemispherical, 60–100 $\mu$  broad and half as high: uredosori epiphyllous, scattered, less than 0.25<sup>mm</sup> in diameter, nearly round, mamillate, dehiscent by central, irregular rupture, the encircling epidermis forming an aecidioid cup, paraphyses peripheral, or also intermixed with the spores; uredospores elliptical or obovate-oblong, 16–21 by 30–40 $\mu$ , wall rather thin, 1.5–2.5 $\mu$ , golden-brown, strongly and evenly echinulate, pores 4–6, equatorial; paraphyses hyphoid, 7–10 by 40–60 $\mu$ , somewhat contorted, smooth, thin-walled, nearly or quite colorless: teleutospores like uredosori, but without paraphyses; teleutospore-heads chestnut-brown, 5–7 cells across, 75–100 $\mu$  in diameter, each spore bearing 4–7 slender, nearly colorless tubercles, 3–4 $\mu$  high; cysts delicate, appressed beneath the head, extending from periphery to pedicel, united laterally; pedicel short, colorless, deciduous.—

On an undetermined species of Mimosaceae, Cardenas, State of San Luis Potosi, Oct. 22, 1898, no. 3144½.

This rust has many characters in common with that on *Pithecolobium*, although the hosts do not appear to be closely related. The host is a thorny shrub or tree, with evenly twice pinnate leaves; the leaflets oblong, nearly glabrous, entire, about 3 by 7<sup>mm</sup>. A cupulate gland usually occurs on the main rachis at the insertion of each pair of petioles.

27. *Ravenelia Pithecolobii*, n. sp.—Uredospores in the teleutospores elliptical or broadly oval, 15–18 by 24–30 $\mu$ , wall golden-yellow, medium thick, 2–3 $\mu$ , thicker at apex, 3–5 $\mu$ , evenly verrucose, pores 4–6, equatorial: teleutospores amphigenous, small, round, at first bullate, scattered, subepidermal, chestnut-brown; teleutospore-heads chestnut-brown, 6–8 cells across, 70–90 $\mu$  in diameter, each spore bearing 2–3 slightly curved tubercles, 5–7 $\mu$  long, acute, pale brownish; cysts appressed beneath the head, extending from periphery to pedicel, united laterally; pedicel colorless, short, deciduous; paraphyses none.—On *Pithecolobium dulce* (Roxb.) Benth., Guadalajara, Sept. 27, 1903, no. 5051.

28. *RAVENELIA MIMOSAE-SENSITIVAE* Henn.—On *Mimosa stipitata* Rob., Cuautla, Morelos, Oct. 28, 1903, no. 5228; and Iguala, Nov. 4, 1903, no. 5326: *M. caerulea* Rose, Cuernavaca, Oct. 30, 1903, no. 5290: *M. Galeottii* Benth., Cuernavaca, Oct. 31, 1903, no. 5303: *M. polyanthoides* Rob., Iguala, Nov. 3, 1903, no. 5324: *M. albida* H. & B., Cuernavaca, Sept. 24, 1898, no. 3125, Oct. 29, 1903, no. 5265; and Cuautla, Oct. 20, 1903, no. 5213: *M. alba floribunda* Rob., Oaxaca, Nov. 10, 1903, no. 5368; Etzatlan, State of Jalisco, Oct. 2, 1903, no. 5086: *Mimosa* sp., Etla, State of Oaxaca, Nov. 16, 1903, no. A.

This species appears to be remarkably uniform on all the hosts so far reported for it. *Uredo sensitiva* Speg. (An. Mus. Nac. Buenos Aires 6:236. 1899) is probably a synonym, judging from the description. All the numbers under this species were submitted to Dr. B. L. ROBINSON of the Gray Herbarium, who determined the hosts.

29. *RAVENELIA CASSIAECOLA* Atk.—On *Cassia* sp., Oaxaca, Nov. 10, 1903, no. 5359.

This species has not before been reported from Mexico, having been known only from the southeastern United States.

30. *Ravenelia inconspicua*, n. sp.—Uredosori hypophyllous, small,  $0.5^{mm}$  or less across, subcuticular, soon naked, pulverulent, ruptured cuticle inconspicuous, paraphyses abundantly intermixed with the spores; uredospores globose or broadly elliptical, 15–20 by  $15-22\mu$ , wall medium thick,  $2-2.5\mu$ , golden-yellow, closely verrucose, pores about 10, scattered, paraphyses spatulate, smooth, cinnamon-brown, paler below, walls thick,  $3-6\mu$ : teleutosori hypophyllous, very small, scattered, blackish, shining, subcuticular; teleutospore-heads chestnut-brown, 6–8 cells across,  $60-100\mu$  in diameter, each cell bearing 4–6 cylindrical tubercles,  $3\mu$  wide by  $5-7\mu$  long, slightly colored; cysts appressed to the under side of the head, 6–10, somewhat united to one another; paraphyses none.—On *Cassia* (or *Caesalpinia*) sp., Zapotlan, State of Jalisco, Oct. 9, 1903, no. 5135.

31. *RAVENELIA SPINULOSA* Diet. & Holw.—On *Cassia Holwayana* Rose (*C. multiflora* Mart. & Gal.), Cuautla, State of Morelos, Oct. 23, 1903, no. 5226; Oaxaca, Nov. 11, 1903, no. 5390: *C. Galeottiana* Mart., Tehuacan, Nov. 7, 1903, no. 5348: *Cassia* sp., Oaxaca, Nov. 10, 1903, no. 5372; Cuernavaca, Nov. 1, 1903, no. 5310.

32. *Ravenelia pulcherrima*, n. sp.—Uredosori amphigenous, in loose groups or scattered, round, small,  $0.25-0.5^{mm}$  across, soon naked, subcuticular, cinnamon-brown, paraphyses numerous, intermixed with the spores; uredospores ellipsoid or oblong-globoid, 15–18 by  $17-24\mu$ , wall thin,  $1.5-2\mu$ , pale golden yellow, finely and closely echinulate-verrucose, pores 6–8, scattered, paraphyses large, capitate or spatulate, 12–18 by  $35-55\mu$ , smooth, walls of the stipe thin and nearly colorless, walls of the head much thickened above,  $3-10\mu$ , chestnut-brown: teleutosori amphigenous, small, scattered or confluent, subcuticular, blackish-brown; teleutospore-heads chocolate-brown, 6–7 cells across,  $75-120\mu$  in diameter, each spore bearing 4–5 inconspicuous papillae, semihyaline,  $1-2\mu$  high; cysts appressed to the underside the head, extending from periphery to pedicel; paraphyses none; pedicel short, colorless, deciduous.—On *Poinciana pulcherrima* L. (*Caesalpinia pulcherrima* Sw.), Yautepec, State of Morelos, Oct. 24, 1903, no. 5236 (type); Iguala, State of Guerrero, Nov. 4, 1903, no. 5337.

33. *RAVENELIA LAEVIS* Diet. & Holw.—On *Indigofera jaliscensis* Rose, Chapala, Oct. 5, 1903, no. 5108: *I. densiflora* Mart. & Gal.,

Cuernavaca, Sept. 26, 1898, no. 3225, Oct. 30, 1903, no. 5292; Oaxaca, Nov. 11, 1903, no. 5380; Amecameca, Oct. 20, 1903, no. 5203; Santa Fé, near City of Mexico, Oct. 18, 1903, no. 5167: *Indigofera* sp., Etzatlán, State of Jalisco, Oct. 2, 1903, no. 5091.

34. RAVENELIA INDIGOFEARAE Tranz.—On *Indigofera cuernavacana* Rose, Cuernavaca, Oct. 30, 1903, no. 5296: *I. Conzattii* Rose, Mt. Alban, State of Oaxaca, Nov. 12, 1903, no. 5392.

35. RAVENELIA BRONGNIARTIAE Diet. & Holw.—On *Brongniartia podalyrioides* HBK., Iguala, State of Guerrero, Nov. 3, 1903, no. 5316.

36. RAVENELIA SIMILIS (Long).—On *Brongniartia podalyrioides* HBK., Guadalajara, Sept. 30, 1903, no. 5181.

37. RAVENELIA TALPA (Long).—On *Cracca Talpa* Rose (*Tephrosia Talpa* Wats.), Guadalajara, Oct. 12, 1903, no. 5151: *C. macrantha* (Wats.) Rose (*Tephrosia macrantha* Wats.), Etzatlán, State of Jalisco, Oct. 2, 1903, no. 5100.

The collection on *C. macrantha* shows some deviation from the type, the tubercles on the teleutospore-heads being larger, and the uredospores being slightly smaller, with germ pores more often scattered.

PURDUE UNIVERSITY,  
Lafayette, Ind.

## ON THE WATER-CONDUCTING SYSTEMS OF SOME DESERT PLANTS.\*

W. A. CANNON.

(WITH TEN FIGURES)

A STATEMENT by VOLKENS<sup>1</sup> to the effect that the ducts of the stems of the shrubs and trees of the Egyptian-Arabian deserts are relatively poorly developed led to an examination of these elements in the shrubs and trees which are growing within reach of the Desert Botanical Laboratory. It appeared at once that our native plants are not poor in water-conducting tissue; on the contrary they are very well provided for in this regard, and I cast about for some means of expressing this condition of affairs from a comparative standpoint. It was especially desired to compare these plants with those of the deserts of Egypt and Arabia, but since the direct comparison was impracticable, because VOLKENS does not give exact data, I have sought a way out of the difficulty by using irrigated desert plants of the species studied as controls. I assume that the desert plants if provided with an abundance of water are for practical purposes mesophytes, and if VOLKENS had in mind the plants of middle Europe, which might well have been the case, we have in this roundabout manner a means of instituting the desired comparison. Aside from this, the great difference in the development of the conductive tissue between desert forms that have been irrigated and those that have not is of considerable interest in itself.

### THE PLANTS STUDIED.

This study includes as many of the native desert trees and shrubs as are readily obtained, and also such as have been irrigated in various places in whatever manner or degree. These are the hackberry (*Celtis pallida*), the creosote bush (*Covillea tridentata*), the candle bush or ocotillo (*Fouquieria splendens*), and a relative of the cruci-

\*Papers from the Desert Botanical Laboratory of the Carnegie Institution. No. 12.

<sup>1</sup> VOLKENS, G., Flora der ägyptisch-arabischen Wüste, p. 82.

fixion thorn (*Zizyphus lycioides*), representing the shrubs; and the cat claw (*Acacia Greggii*), the mesquite (*Prosopis velutina*), and two species of palo verde (*Parkinsonia microphylla* and *P. Torreyana*), representing the trees.

These plants grow in habitats which are very unlike in appearance, and which presumably are dissimilar also in such fundamentals as soil characteristics and water supply. Speaking now of the vicinity of the Laboratory only, for a radius of about ten miles the habitats may be classed as (1) mesa, (2) river bottoms, (3) the rocky slopes of the lower mountains, and (4) the "draws" of these mountains. As regards the amount of water in the soil available to the plants, the river bottoms should be classed first, after which should be placed the draws; the rocky slopes and the mesa are frequently very dry. The mesa is peculiarly desertic, because a subsoil, the so-called "calliche," which is practically impervious to water, reaches within a few inches of the surface of the ground. The top soil, the adobe, is a clay. In the river bottoms the top soil is several feet in depth.

The mesquite and the cat claw are found especially on the bottom lands, where they may attain the size of forest trees, especially the former. Both of these trees adapt themselves to the drier habitats, however; but in such places they are of much smaller size and are gnarled and much changed in outward appearance. *Celtis* and *Zizyphus* also grow on the river bottoms; *Fouquieria* seems to be confined to the rocky slopes. *Parkinsonia microphylla* also is mostly found on rocky or well-drained slopes, while the other species of palo verde (*P. Torreyana*) is to be found in the draws at a lower level. Finally, the creosote bush, which is the characteristic shrub of the mesa, grows on the bottoms as well as on the mesa, and is there large and most vigorous. The natural distribution of these plants, and also the modification in form which they assume in the various habitats, point to the conclusion that the optimum conditions for them are attained where, other conditions being equal, water is to be had in abundance.<sup>2</sup>

That the greater vigor of the plants on the river bottom, as opposed to those on the mesa, for instance, is not due mainly, if at all, to

<sup>2</sup> Compare "The creosote bush (*Covillea tridentata*) in its relation to water supply," V. M. SPALDING, BOT. GAZETTE 38:124. 1904.

differences in the character of the soil, is shown by the manner in which they react to an abundance of water when they are well irrigated, the substratum being otherwise the same. The creosote bush and both species of palo verde thrive equally well by the side of the same irrigating ditch, and the same is true of the other plants mentioned above. That is to say, each of these plants, whatever may be their natural habitat, is most vigorous where the water supply is adequate. The suggestion cannot be avoided, therefore, that the distribution of these plants in this vicinity is in some way indicative of their specific reaction to the minimum rather than to the optimum supply of water. The extent to which this phase of the reaction of desert plants to water may influence their present distribution in this vicinity will be the subject of future experimental investigation at the Laboratory.

As has been suggested above, the irrigated desert plants are the more vigorous in every way. The leaves are larger and are functional for a longer period, and the plants attain also much larger proportions than those that are not irrigated, and they also grow faster. To give but a single instance of the latter, a palo verde well-irrigated four years from the seed is now about eight feet high, while there are many of these trees in the neighborhood of the Laboratory, without doubt many times as old, that are not so high.

With the larger leaf surface of the irrigated plants one would look for a faster rate as well as for a larger total transpiration. Whatever may be the absolute transpiration of the irrigated forms, the structure of the stems of the irrigated as opposed to the non-irrigated plants indicates that the latter have the faster rate. That is, the non-irrigated stems have larger ducts and more of them per equivalent area of cross section than the irrigated stems, which can be taken as indicating the more rapid transpiration of the former.<sup>3</sup>

To anticipate the general conclusions to be drawn from this paper, we may therefore be justified in thinking that the desert plants of this locality, being probably better provided with conductive elements than those of the Egyptian-Arabian deserts, may also have a faster rate of transpiration.

<sup>3</sup> PFEFFER, *Physiology of plants* 1: p. 216; HABERLANDT, *Pflanzenanatomie* (3d ed.), p. 288.

## THE METHODS AND THE RESULTS.

The number of ducts of the woody cylinder was determined in the following manner and under the following conditions: The branches selected for study were as nearly of the same size as possible, namely  $0.6\text{ cm}$  in diameter; it did not appear feasible to get them all of the same age. All of the sections were made midway between the nodes. In counting the ducts an arbitrary area as a standard of comparison was taken as follows. A circle  $14\text{ cm}$  in diameter was drawn on metric paper and octants were struck off. By means of an Abbé camera lucida an image of the section was so thrown on the metric paper that the periphery of the woody cylinder and the two points delimiting any octant coincided. The standard octant had an area of  $19.24\text{ sq cm}$  ( $14^2 \times 0.7845 \div 8$ ). Since the magnification employed was 66 diameters, the area actually examined was  $0.29\text{ sq cm}$ , or  $29\text{ sq mm}$ .

The method of studying the ducts thus chosen gives the greatest prominence to the latest growth. This was desired for the reasons that the most active transfer of water probably takes place in the more peripheral ducts, and because I could be most sure of the recent history of the plants as regards irrigation.

The term "irrigated" as used in this paper needs a word of explanation. I have been obliged to take whatever plants I might find that had received any water in addition to the rains. In certain instances, to be detailed below, the plants were growing by the side of an irrigating ditch and without question had water in abundance every day of the year. In other cases they were a greater or less distance from the ditch; and in yet other instances the ditch was filled with water for a portion only of the time, say once a month, during the dry season. Some of the forms received little water artificially, as, for example, *Zizyphus*, which is in the cactus garden at the University of Arizona and is not irrigated oftener than once or twice in a year. When the plants received a small amount of water I have called them "semi-irrigated." The distinction between irrigated and semi-irrigated forms is thus purely arbitrary.

The accompanying table presents a summary of the study. The numbers refer to the number of ducts in  $29\text{ sq mm}$  of stem cross section made under the conditions described above.



	Not irrigated	Irrigated	Semi-irrigated
<i>Acacia Greggii</i> .....	41	..	23
<i>Celtis pallida</i> .....	51	42	..
<i>Covillea tridentata</i> .....	80	20	..
<i>Fouquieria splendens</i> .....	215	..	85
<i>Parkinsonia microphylla</i> .....	19	10 <sup>4</sup>	..
<i>Parkinsonia Torreyana</i> .....	28	23 <sup>4</sup>	..
<i>Prosopis velutina</i> .....	51	25 <sup>4</sup>	..
<i>Zizyphus lycioides</i> .....	44	..	39

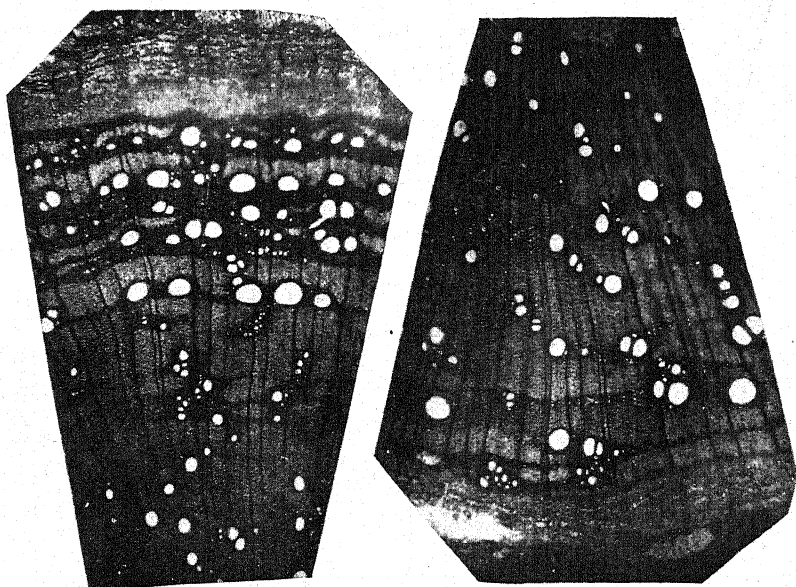


FIG. 1.—*Acacia Greggii*: left, not irrigated; right, irrigated.

The following outline indicates some of the conditions of growth of the plants studied.

*ACACIA GREGGII* (fig. 1).—The non-irrigated specimen was taken by the roadside between an old and at present unused irrigating ditch and the road ditch. Water stands in the latter for a considerable period after each heavy rain, and thus the effects of the rain are considerably prolonged. The irrigated form was growing about 6<sup>m</sup> from a ditch in which the water flows the most or perhaps all of the year. The older portion of the non-irrigated stem does not

<sup>4</sup> The ducts of the irrigated plants were very small; see figs. 5, 6, 7.

have as many ducts as the more recent, an indication according to the present view that this plant might formerly have been irrigated. The owner of the field in which the non-irrigated specimen is found tells me that such, indeed, is the case.

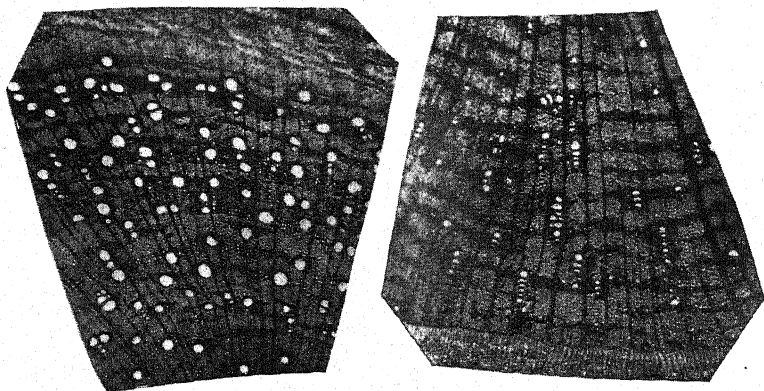


FIG. 2.—*Celtis pallida*: left, not irrigated; right, irrigated.

*CELTIS PALLIDA* (fig. 2).—The non-irrigated plant grows on the mountain on which the Desert Laboratory is situated. The irrigated

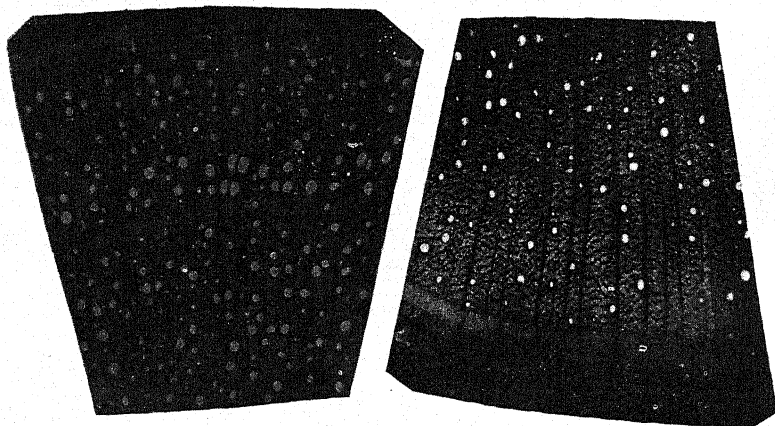


FIG. 3.—*Covillea tridentata*: left, not irrigated; right, irrigated.

plant is on the grounds of the University of Arizona, and has been watered occasionally.

*COVILLEA TRIDENTATA* (fig. 3).—The non-irrigated plant is on the mesa at the northern base of the laboratory mountain. The

irrigated plant is growing by an irrigating ditch. Its roots are without question in a soil which is saturated with water all of the year. A third specimen, not figured, was originally chosen for study as being representative of the irrigated form. It was placed near an irrigating station and was supposed, therefore, to have received considerable water. When I examined the conductive system of this plant I found it to be essentially the same as the non-irrigated specimen. It was learned on inquiry that the plant had not been

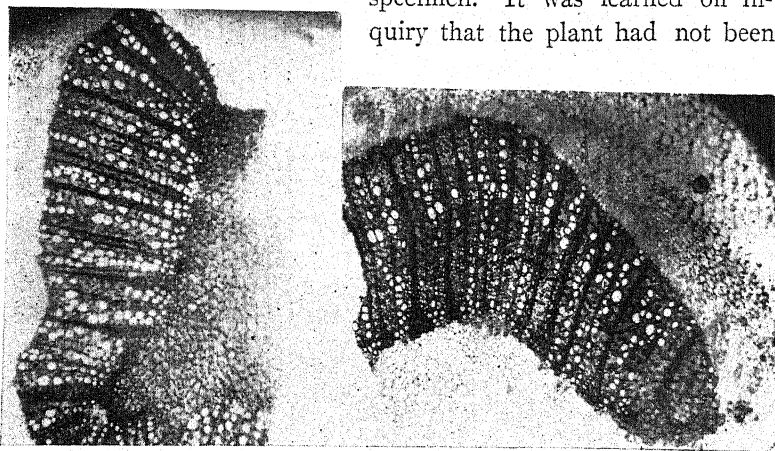


FIG. 4.—*Fouquieria splendens*: left, not irrigated; right, irrigated.

irrigated at all, a curious confirmation of the view advanced in this paper.

*FOUQUIERIA SPLENDENS* (fig. 4).—The non-irrigated specimen is growing on the mountain near the Laboratory. The irrigated is on the grounds of the Indian Industrial School, Tucson. It has received a variable amount of water, more during the past two years than formerly.

*PARKINSONIA MICROPHYLLA* (fig. 5).—The plant that is not irrigated is on the mesa at the northern base of the Laboratory mountain. The irrigated specimen is on the campus of the University of Arizona and has been irrigated frequently.

*PARKINSONIA TORREYANA* (fig. 6).—The non-irrigated palo verde is in the draw at the western base of the Laboratory mountain.

The irrigated plant is on the campus of the University of Arizona and has been irrigated in the same manner as the other species of palo verde given above.

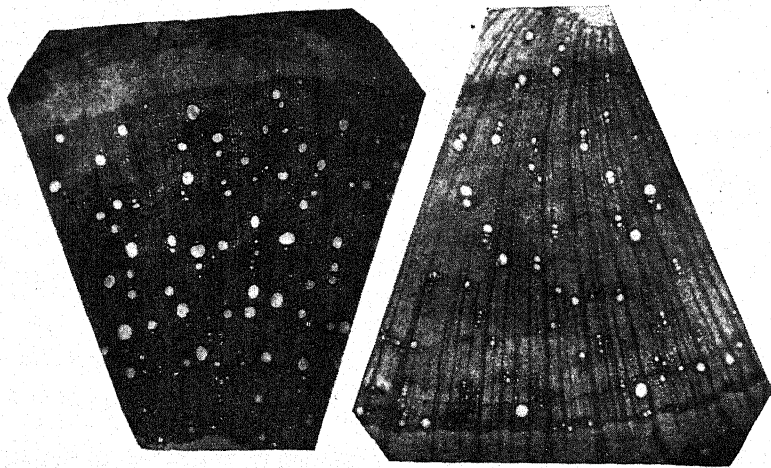


FIG. 5.—*Parkinsonia microphylla*: left, not irrigated; right, irrigated.

*PROSOPIS VELUTINA* (fig. 7).—The non-irrigated specimen of mesquite is growing near the Laboratory. It is about 2<sup>m</sup> high,

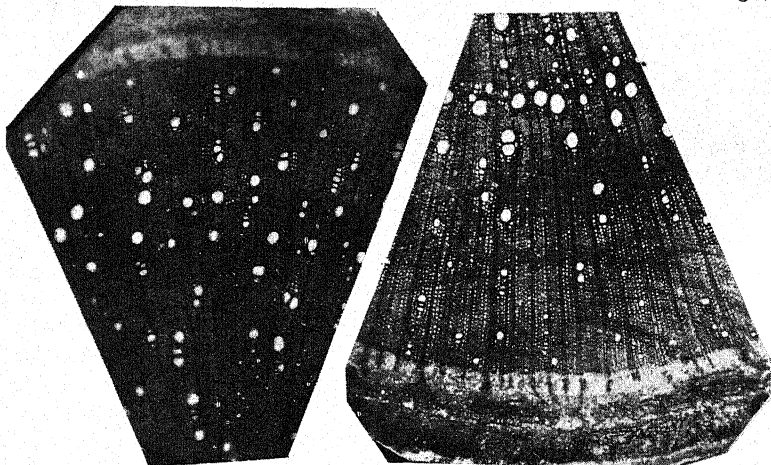


FIG. 6.—*Parkinsonia Torreyana*: left, not irrigated; right, irrigated.

gnarled, and evidently in need of a better supply of water. The irrigated form of mesquite is growing near an irrigating ditch in

which there is water several times during the year; not continuously as in the other ditch mentioned above.

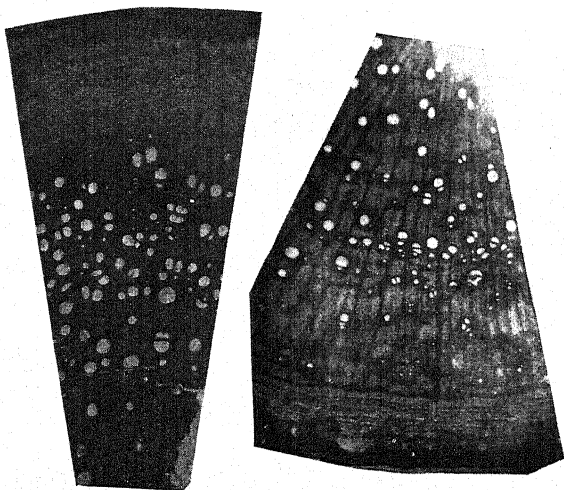


FIG. 7.—*Prosopis velutina*: left, not irrigated; right, irrigated.

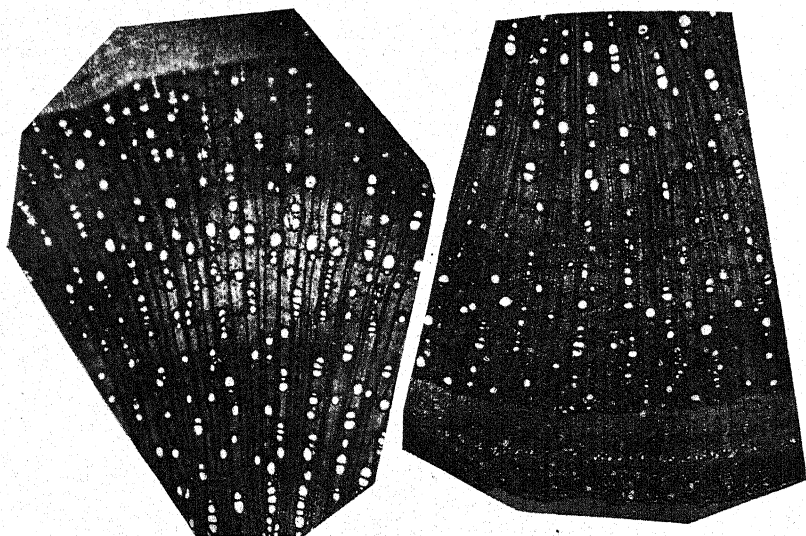


FIG. 8.—*Zizyphus lycioides*: left, not irrigated; right, irrigated.

*ZIZYPHUS LYCIOIDES* (fig. 8).—The non-irrigated plant is on the mesa near Tucson. The irrigated plant is growing on the campus

of the University of Arizona in the cactus plantation. It receives water by direct application about twice a year. The nearest irrigating ditch is across the drive, about 13<sup>m</sup> distant. It should be explained that the drive is so constructed with reference to the underlying caliche that presumably no water seeps across.

#### GENERAL CONCLUSIONS.

Although, much to my regret, the amount of water given to the irrigated plants is not known with any degree of exactness in any case, there can be no mistaking the fact that branches of irrigated plants (even if "semi-irrigated" only) are poorer in conductive tissue than branches of the same diameter of non-irrigated plants. This is an unexpected condition and of especial interest in view of the small development of the water-conducting elements in the non-irrigated forms of the Egyptian-Arabian deserts as given by VOLKENS. It merits further investigation.

Without doubt the irrigated plants have a greater absolute transpiration and organize each year a larger amount of wood than the non-irrigated plants of the same age; but the composition of the wood is different in the two instances. The irrigated plants construct a relatively large amount of non-conductive tissue each year (as compared with the amount of the other wood elements formed), while the reverse is true of the non-irrigated plants. So that it happens, in stems of equal diameter but not of the same age, that the non-irrigated and older stems have more vessels than the irrigated and younger. One other characteristic of non-irrigated stems was also noted, namely, their ducts were usually or frequently of greater diameter.

We find, therefore, a quantitative and a qualitative difference in the structure of irrigated and non-irrigated stems, and from what has been stated it appears that any adequate account of the causes which induce these structural peculiarities must separate the processes which may be associated with the formation of the woody cylinder as a whole from those which may be connected with the organization of that part of the wood that is primarily to conduct water.

I shall not presume at present to offer any hypothesis to explain

the phenomena noted. It seems, however, on the surface of things, that such explanation must take into consideration the differences in the length and the character of the growing season of the two classes of plants. The irrigated plants probably do not cease growing during any month of the year and are most active when the temperature is also the highest.

The curve of the growth of these plants probably is very nearly parallel to that of the temperature for the year. The non-irrigated plants are subject to the peculiar climatic conditions of the desert. The summer is the season of the maximum temperature. At Tucson there are each year two rainy seasons: that of winter, January-February; and that of summer, July-August. The period of the greatest vegetative activity occurs at the time of the midsummer

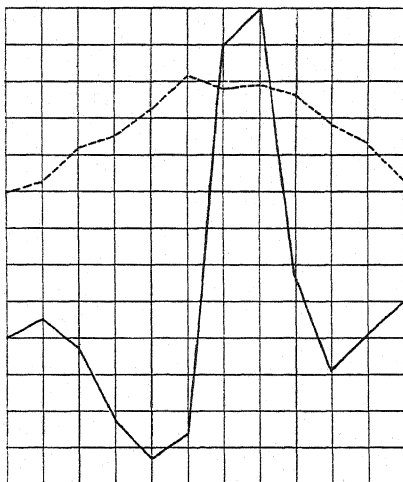


FIG. 9.—Mean yearly rainfall and maximum temperature at Tucson; broken line is temperature ( $1^{\text{cm}} = 10^{\circ}\text{F.}$ ); solid line is rainfall in inches ( $1^{\text{cm}} = 0.2^{\text{in.}}$ ).

rains (it is not known how the winter rains affect the growth of these forms), and all growth ceases very soon after the rains are over. The curve of growth of the non-irrigated plants would be very similar, no doubt, to that for the yearly rainfall. *Fig. 9* expresses in a graphic manner the annual rainfall and temperature at Tucson. It may be taken also to indicate the rate of growth of the non-irrigated and the irrigated desert plants.

Whatever may be the effect in detail, it must be admitted, I think, that the growth of the non-irrigated plants, and this may also be true of their transpiration, is directly associated with the distribution of the annual rains. Further, the intensity of this growth, as indicated by the structure of these plants and the general vegetal conditions of the desert, is probably directly connected with the fact that the

heaviest rainfall occurs in summer. These facts encourage the view that the peculiar structure of the plants of the Egyptian-Arabian deserts, as regards the points under consideration, may likewise be due wholly or in part to analogous causes.

The climate of these foreign deserts is quite different from that

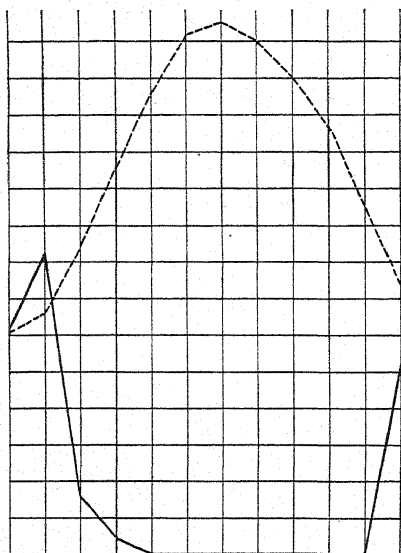


FIG. 10.—Rainfall and temperature at Cairo, Egypt, in 1887; broken line is temperature ( $1^{\text{cm}} = 2^{\circ}\text{C}.$ ); solid line is rainfall ( $1^{\text{cm}} = 1\text{mm}.$ )

of the desert about Tucson in the distribution, as well as the amount, of the annual rainfall; and consequently in the relation of the rainfall to the period of the highest temperature. The most rain occurs in the deserts of northwestern Africa and southwestern Asia in winter, but the maximum temperature is in summer.

The period of the greatest vegetative activity in these deserts is in winter; in summer the plants are dormant. In the Egyptian-Arabian deserts, therefore, the renewal of growth occurs at the time of the year when the rainfall is also greatest, but not at the season of the highest temperatures. The curve of growth of the plants of this region probably coincides very accurately with the curve of the yearly rainfall. I have no means at hand of telling whether, on the other hand, if such plants were irrigated the period of their greatest growth would fall in summer. Such is apparently the case with some of the cultivated forms<sup>5</sup> in deserts farther west.

*Fig. 10* represents the relation of the yearly rainfall to the temperature at Cairo, for the year 1887.

<sup>5</sup> SWINGLE, W. T., *The date palm*. U. S. Dept. Agric. 1904.



## THE EFFECTS OF TOXIC AGENTS UPON THE ACTION OF BROMELIN.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY.

LXXIII.

JOSEPH STUART CALDWELL.

### HISTORICAL.

ATTENTION was first directed to the existence of a proteolytic enzyme in the juice of the pineapple (*Ananas sativus*) by MARCANO (13). It was called bromelin by CHITTENDEN, who, with his pupils, examined it in some detail (3, 4). They prepared it from the expressed and filtered juice, after neutralization, by saturation with crystals of ammonium or magnesium sulfate or sodium chlorid, any of which precipitate the enzyme together with some proteid matter. The precipitate was dialyzed free from salt in running water, collected upon a filter, and dried at 40° C. upon a water-bath. The flaky, whitish residue thus obtained consisted of the enzyme with some associated proteid. It was soluble in water and active in acid or neutral solutions, very slightly or not at all in an alkaline medium. The sodium chlorid preparation was more active and greater in amount than the others, and was used throughout the experiments. CHITTENDEN'S study was directed principally to a determination of the products of digestion of blood-fibrin, myosin, and coagulated egg albumen. These were found to be hemi- and anti-peptones, proto-, hetero-, and deuterio-proteose, leucin, and tyrosin. The enzyme was thus determined to be tryptic in nature, and akin to other vegetable trypsins in that it acted best in an acid medium.

### PURPOSE.

The experiments described in this paper were undertaken with a view to ascertaining whether a similarity existed between the effects of poisonous metals upon the action of an enzyme and those observed in experiments upon living organisms. While an immense amount of work has been done with plants and animals, the results are at variance, not even agreeing as to the most poisonous metal.

It was hoped that the limits of toxicity might be more clearly defined in the case of enzymes.

Very little work has been done in this field. In a general way it is known that slight amounts of metallic salts affect enzymic action. COLES (6) found that cations and hydroxyl ions depress and anions accelerate the action of ptyalin and invertin. Results with acids and alkalis vary with the enzyme used (7, 8, 10). So far as I am able to ascertain, the only extended work with poisonous metals has been that of MCGUIGAN (16) upon diastase. His results confirm the theory advanced by MATHEWS (10, 11) that the physiological action of any atom or ion depends primarily upon its affinity for its electrical charge. The work described in this paper was undertaken with a view to determining whether this theory would hold for a tryptic enzyme, and was completed before MCGUIGAN's results were known to me.

Bromelin was chosen as a typical vegetable trypsin, rapid in its action, easily prepared, and hitherto studied only with reference to its digestion-products and its action in the presence of acids and alkalis.

#### PREPARATION OF THE ENZYME.

It was desirable to prepare the enzyme in as pure a state as possible, since it was early found that the presence of associated proteid matter obscured the results of my experiments. Even very slight amounts apparently shielded the enzyme from the action of poisons. Furthermore, it was shown by some preliminary experiments, summarized elsewhere in this paper, that autodigestion, with the formation of peptones, leucin, and tyrosin, occurred in solutions of the impure enzyme when kept for some time at temperatures between 25 and 65° C.

After several trials, a preparation was obtained which contained only very slight traces of associated proteid, and which was not at all autodigestive. The dialyzed NaCl-precipitate was dissolved in a little water, reprecipitated by the addition of 95 per cent. alcohol, again dissolved in water, and again precipitated by adding crystals of  $(\text{NH}_4)_2\text{SO}_4$ . A little of the associated proteid is left behind at every precipitation, and five repetitions of the process gave a preparation containing only slight traces of proteid. Precipitation was much hastened by placing the vessel in the refrigerator at about 4° C.

After being dried upon the water-bath at 40° C., the preparation was wholly soluble in water and was not autodigestive in any medium even after prolonged standing. It was active in faintly acid or alkaline solutions, though not at all in neutral media. This preparation was used throughout the experiments.

In order that the results might not be rendered inaccurate through the use of preparations of unequal purity, all the enzyme used was prepared at one time and thoroughly mixed after drying. From 46 pineapples of average size, 16.4<sup>kg</sup> of filtered juice were obtained, which yielded 14.8<sup>gm</sup> of the enzyme dried at 40° C. This was kept in a calcium chlorid desiccator and from time to time compared with fresh preparations, but no deterioration occurred in the period covered by the experiments.

The enzyme was most active in solutions of alkalinity equaling  $m/30$ – $m/40$  NaOH, and was considerably less active in acid solutions irrespective of strength. Its action was wholly inhibited by  $m/10$  HNO<sub>3</sub>, or H<sub>2</sub>SO<sub>4</sub>,  $m/15$  HCl, NaOH, or KOH, or  $m/20$  NH<sub>4</sub>OH.

The fact that the enzyme had been found most active in acid and neutral solutions by CHITTENDEN, while my own preparations were markedly more active in alkaline than in acid media and showed only the slightest trace of activity in neutral solutions, led me to a very careful examination of this point. CHITTENDEN's statement of his method was followed in making a number of preparations. Pineapples of varying ripeness were chosen, upon the hypothesis that a change in the nature of the enzyme might occur with the ripening of the fruit, but all of my preparations agreed perfectly in requiring an alkaline medium for optimum action, very much less action occurring in acid media. One preparation from very immature fruits showed faint activity in a neutral solution. This difference from the results of CHITTENDEN's examination seems explicable only on the ground that I have misunderstood his statement of his method of preparation; yet the method is simple and the statement is apparently lucid and exact enough to be followed without difficulty.

#### ISOLATION OF THE ALKALINE ENZYME.

Some of the facts observed in the preparation of the enzyme suggested that it might be in reality a mixture of two enzymes separ-

able by proper treatment. Some experiments with this purpose in view met with partial success.

A neutral solution of one gram of the dry enzyme in 100<sup>cc</sup> water was carefully heated to 65° C. Upon gradual addition of NaCl crystals a slight precipitate settled out, which when collected by filtering, and dried, weighed 0.31<sup>gm</sup>. The filtered liquid when freed from NaCl showed no activity upon egg-albumen in acid solutions, regardless of strength, but its activity in alkaline solutions was undiminished and accorded in all respects with that of ordinary preparations of the enzyme in alkaline media, the products of digestion with the two being identical. The heat precipitate was imperfectly soluble in water and showed no action upon egg-albumen in any medium.

I believe that these facts, with the differences, elsewhere stated, in the action of poisons upon acid and alkaline solutions of the enzyme, justify the conclusion that there are present in the preparation two enzymes, one active in acid, the other in alkaline solutions. I am aware that full proof of this statement demands isolation of the acid-enzyme without destroying it in the process, but this I am as yet unable to do.

That the presence of NaCl is a necessary condition for the precipitation of the acid-enzyme is shown by the fact that no precipitation occurs in unsalted solutions until heated to 76° C., activity in both acid and alkaline media being retained until complete precipitation occurs at 87-90°.

#### EXPERIMENTS WITH POISONS.

In the experiments with poisons, solutions containing 0.006<sup>gm</sup> of the enzyme per cubic centimeter were made up with distilled water previously made acid or alkaline by the addition of HCl or NaOH. An  $m/32$  acid or alkali was adopted as a medium for all digestions, since this strength allowed optimum activity in each case. Thymol was used to prevent bacterial infection and was found perfectly satisfactory. Of this solution 5<sup>cc</sup>, containing 0.03<sup>gm</sup> of the enzyme, were transferred to each of the test-tubes to be used. To each was then added 5<sup>cc</sup> of the poison to be used, of twice the desired strength, *i. e.*, 5<sup>cc</sup> enzyme solution plus 5<sup>cc</sup>  $m/5000$   $\text{Ba}(\text{NO}_3)_2$  gives

10<sup>cc</sup> *m*/10000 Ba(NO<sub>3</sub>)<sub>2</sub>. To each tube was then added 1<sup>gm</sup> egg-albumen previously boiled and granulated, and the tubes were then placed in the water-bath at 40° C. for 24 hours. They were then removed, filtered to remove undissolved albumen, and tested.

Tests were made for peptones, leucin, and tyrosin by all the standard tests. The biuret reaction after precipitation of the albumoses, and the tryptophan reaction described by VINES (25, *d*) were

SALT	OPTIMUM ACID MEDIUM <i>m</i> /32 HCl		OPTIMUM ALKALINE MEDIUM <i>m</i> /32 NaOH	
	Dilution of molecular solution		Dilution of molecular solution	
	Inhibiting	Allowing	Inhibiting	Allowing
AgNO <sub>3</sub> .....	110,000	130,000	80,000	100,000
Ag <sub>2</sub> SO <sub>4</sub> .....	80,000	110,000	80,000	96,000
CuSO <sub>4</sub> .....	60,000	90,000	45,000	60,000
CuCl <sub>2</sub> .....	48,000	70,000	40,000	54,000
HgNO <sub>3</sub> .....	75,000	90,000	64,000	80,000
Hg(NO <sub>3</sub> ) <sub>2</sub> .....	65,000	85,000	45,000	60,000
Pb(NO <sub>3</sub> ) <sub>2</sub> .....	40,000	60,000	36,000	56,000
PbCl <sub>2</sub> .....	37,500	56,000	40,000	56,000
Zn(NO <sub>3</sub> ) <sub>2</sub> .....	28,000	32,000	16,000	22,000
ZnSO <sub>4</sub> .....	16,750	23,000	14,000	17,000
Ba(NO <sub>3</sub> ) <sub>2</sub> .....	10,000	13,000	6,000	8,000
BaCl <sub>2</sub> .....	8,000	12,000	6,000	7,500
Cd(NO <sub>3</sub> ) <sub>2</sub> .....	6,000	7,600	5,000	7,000
CdSO <sub>4</sub> .....	4,800	6,650	4,750	5,650
Co(NO <sub>3</sub> ) <sub>2</sub> .....	4,800	6,400	3,000	4,000
CoSO <sub>4</sub> .....	4,500	5,500	3,000	3,600
LiNO <sub>3</sub> .....	1,000	1,400	900	1,200
Li <sub>2</sub> SO <sub>4</sub> .....	750	1,050	600	900
Na <sub>2</sub> SO <sub>4</sub> .....	512	1,024	500	750
NaNO <sub>3</sub> .....	1,600	2,000	1,100	1,675
Sr(NO <sub>3</sub> ) <sub>2</sub> .....	900	1,200	720	960
SrSO <sub>4</sub> .....	750	1,100	650	1,050
SrCl <sub>2</sub> .....	800	1,000	600	900
Mg(NO <sub>3</sub> ) <sub>2</sub> .....	650	1,000	320	512
MgSO <sub>4</sub> .....	600	1,000	375	512
KCl.....	100	160	60	120
KNO <sub>3</sub> .....	100	200	125	175
(NH <sub>4</sub> ) <sub>2</sub> SO <sub>4</sub> .....	256	512	256	432
NH <sub>4</sub> NO <sub>3</sub> .....	400	512	256	432
NH <sub>4</sub> Cl.....	320	480	275	420

found to be most delicate, HOFFMANN's and SCHERER's tests being used as confirmatory. The unequal delicacy of the reactions employed made it necessary to adopt a rule to secure uniformity in results. Hence only such concentrations were considered inhibiting as gave no results with any test, while the only strengths tabulated as allowing

action were those that gave unmistakable results with a majority of the tests. SCHERER'S test—the isolation of leucin and tyrosin—was of course conclusive. The application of this rule resulted in some cases in comparatively wide gaps between the toxic and non-toxic strengths given in the table; *e. g.*,  $m/650$   $\text{Mg}(\text{NO}_3)_2$  is given as inhibiting, since it gave none of the tests;  $m/1000$  as allowing action, since it gave all; while  $m/850$  gave faint tryptophan reaction but no SCHERER'S test, and was therefore disregarded.

In beginning to experiment with a particular salt, a stock solution was first made; a portion of this was diluted to give the greatest strengths desired, and greater dilutions were made from this by successive additions of distilled water. For example, in my first experiment with  $\text{CuSO}_4$  a series of tubes with  $m/5000$ ,  $m/10000$ , up to  $m/400000$  were made up in duplicate. The results indicated where the critical points—between  $m/50000$  and  $m/100000$ —were to be expected, the duplicates preventing error. Closer series were then made and repeated until the limits of toxicity and non-toxicity were clearly determined. Finally the whole table was twice checked over in duplicate, so that the figures given represent in every case from eight to twelve concordant results.

The results obtained may be shown by arranging the metals used in the order of toxicity, beginning with the most poisonous. The results obtained by MATHEWS, working with eggs of *Fundulus heteroclitus*, and those of MCGUIGAN with diastase are given for purposes of comparison.

MATHEWS (14)	MCGUIGAN (16)	CALDWELL
Ag	Ag	Ag
Hg	Hg	Hg
Cu	Cu	Cu
Cd	Cd	Pb
Pb	Co	Zn
Zn	Zn	Ba
Co	Pb	Cd
Li	Sr	Co
Sr	Ba	Na
Na	Mg	Li
Ba	Li	Sr
Mg	Na	Mg
$\text{NH}_4$		$\text{NH}_4$
K		K

While there are a number of exceptions, these results show a general agreement which is more striking in view of the total lack of harmony in the earlier work with poisons, whether with plants or animals. Silver, mercury, and copper stand at the head of the three lists. In my experiments, cadmium stands near zinc, nearly in the place it should occupy in accordance with the theory of MATHEWS, who found it in his work only less poisonous than copper. MATHEWS and MCGUGAN have found sodium less poisonous than lithium or strontium, using the chlorids. I find the three sulfates practically equal in toxicity, while sodium nitrate is much more poisonous than the other nitrates. My results agree more nearly with those of MATHEWS in the places given lithium, lead, and cobalt. The great toxicity of barium in my experiments cannot be attributed to impurities in the salts used or to inaccuracy in performing the experiments, since several standard preparations gave markedly uniform results, and the series has been worked over so many times that the possibility of mistake is excluded.

The nitrates uniformly inhibit the action of the enzyme in somewhat greater dilution than the corresponding sulfates and chlorids, which agree very closely.

The action of the enzyme is markedly weaker and is uniformly inhibited by poisonous solutions of less concentration than when acting in alkaline media. This confirms the evidence already given for the existence of two enzymes.

#### EXPERIMENTS UPON AUTODIGESTION.

The experiments upon autodigestion were suggested by the discovery that while none of the tests for peptones, leucin, or tyrosin were given by freshly prepared aqueous solutions of the impure enzyme, all these were present in such solutions after standing for a little time at 25–60° C. CHITTENDEN (*loc. cit.*) has stated that the proteids of the juice are exceedingly resistant to the action of the enzymes, while VINES (25, e) has mentioned the occurrence of autodigestion in the expressed juice. My own observations led to the supposition that the associated proteids were acted upon by the enzyme at suitable temperatures. This was found to be true of acid and alkaline solutions, not of neutral ones. The associated proteid

was first rapidly digested, the breaking down of the enzyme itself proceeding more slowly and continuing until complete.

Solutions containing 1<sup>gm</sup> each of the impure enzyme were placed in the water-bath and kept at 40° C. for 12 days, the growth of bacteria being prevented by the addition of thymol. At short intervals, portions were removed and examined for digestion products by all the methods employed in other experiments. Traces of peptones, leucin, and tyrosin were found after 1½ hours, rapidly increased in amount for 10–14 hours, then very slowly increased for 9–10 days. During the first day, portions were hourly removed, filtered, and tested as to their activity upon egg-albumen, no perceptible decrease in power being shown. After the first day, portions were removed once or twice daily and tested, and there was found a decrease in power to digest egg-albumen proceeding *pari passu* with the increase of digestion products in the stock solution, until after the eighth day no perceptible action upon egg-albumen occurred, even after prolonged standing. Contrary to my expectation, the process of autodigestion was not checked or inhibited by the accumulation of its products, since it was equally rapid in the stock solution and in another from which the digestion products were daily removed. Furthermore, the two enzymes break down with equal rapidity, since activity in acid and alkaline media decreased equally until the eighth day, after which no action occurred.

No such decrease in activity occurred, nor were digestive products present, in purer preparations of the enzyme kept for a much longer period (five weeks) under similar conditions, nor were such solutions affected by light.

It was hoped that a preparation purer than I had otherwise been able to make might be obtained by allowing the digestion to proceed until the associated proteid had been broken down, separating the products of digestion from the enzyme and drying the latter. To my surprise, digestion immediately began in aqueous solutions made from such a preparation, and would occur perceptibly in the moist precipitate while drying in a calcium chlorid desiccator.

Autodigestion does not begin so long as there are present proteids, either egg-albumen, fibrin, or that present in the juice, but does begin as soon as these have been broken up.



Autodigestion occurs most rapidly in alkaline solutions equaling  $m/16$ – $m/32$  KOH or NaOH, less rapidly in  $m/10$ – $m/24$  HCl,  $H_2SO_4$ , or  $HNO_3$ . Action was inhibited by greater concentrations and occurred more slowly in weaker ones. It occurs with poisons in strengths very much greater than those inhibiting the action of purer preparations upon egg-albumen, as shown by the following table:

AUTODIGESTION IN  $m/24$  HCl AT  $40^\circ$  C.

SALT	DILUTION OF MOLECULAR SOLUTION	
	Inhibited	Allowed
$(NH_4)_2SO_4$ .....	72	120
$NH_4NO_3$ .....	48	64
$Mg(NO_3)_2$ .....	128	256
$MgSO_4$ .....	100	175
$CuSO_4$ .....	6,000	8,650
$AgNO_3$ .....	16,000	22,750
$ZnSO_4$ .....	10,000	16,000
$Sr(NO_3)_2$ .....	600	800
$Cd(NO_3)_2$ .....	512	768
$CoSO_4$ .....	1,600	2,400
$NaSO_4$ .....	150	225

In an alkaline medium ( $m/32$  NaOH), inhibiting and allowing strengths were uniformly about one-third greater with the few salts tested.

The table just given also represents pretty closely the conditions for the digestion of egg-albumen by such impure preparations, in so far as this was studied. For example, digestion would just occur in  $m/14000$   $ZnSO_4$ ,  $m/7200$   $CuSO_4$ , or  $m/1800$   $Co(NO_3)_2$ , as determined by decrease in the amount of albumen subjected to the test. Hence the degree of susceptibility to poisons is determined largely by the purity of the preparation employed, apparently because the enzyme is shielded by the associated proteid from the action of poisons. The results obtained with preparations of varying purity are parallel, *i. e.*, the toxic strengths of different metals bear approximately the same relation to each other irrespective of the preparation used.

## SUMMARY.

1. Impure preparations of bromelin are strongly autodigestive in acid or alkaline media, such digestion beginning when the breaking up of proteid impurities has been completed and proceeding to total destruction of the enzyme.

2. The effects of poisons vary with the purity of the preparation used, slight amounts of proteid impurities rendering necessary an enormous increase of concentration in order to inhibit action.

3. The toxic strengths of the salts used maintain a constant relationship irrespective of the purity of the enzyme used, *i. e.*, silver is always most poisonous, copper third, zinc sixth, and so on.

4. Bromelin, when prepared in a relatively pure condition is not at all autodigestive, the presence of some proteid of the juice apparently being a prerequisite for such action.

5. Such preparations appear to be in reality a mixture of two enzymes, one active in alkaline solutions, slightly more resistant to poisons, and twice as great in amount as the other, which is active in acid media and is destroyed by heating to 65° C. in saline solution.

6. The limits of toxicity and non-toxicity are somewhat more clearly defined than has been the case in experiments upon living organisms (5, 11, 12, 18, 19, 25).

7. The results obtained agree in general with MATHEWS's arrangement of the metals upon the theory that "the affinity of the atom or ion for its electrical charge is the main factor determining its physiological action." Cadmium in my experiments occupies the position it should hold in accordance with this theory, while barium is far out of place.\*

My sincere thanks are due to Dr. B. E. LIVINGSTON, at whose suggestion the work was begun, for much help in its inception, and to Dr. C. R. BARNES for assistance in its progress and completion.

\*Experiments undertaken in order to determine more conclusively the place to be given barium are still in progress. I have found it only relatively less poisonous than zinc in every case, whether bromelin, papain, or animal trypsin were the enzyme used.

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## BRIEFER ARTICLES.

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### THE EARLY HISTORY OF ANGIOSPERMS.

THE paper lately published by Mr. HAROLD LYON on the embryo of angiosperms<sup>1</sup> gives a clear account of existing views on the race-history of monocotyledons and dicotyledons. In the course of his argument Mr. LYON has referred to my own work on the subject in very generous terms, while giving in greater detail than before the arguments which had already led him to the opposed conclusion. We are, as before, in complete agreement as to the field of battle. We both hold that monocotyledons and dicotyledons come from a common stock, and that the single cotyledon of the one is strictly homologous with both cotyledons of the other. But on the question of the comparative antiquity of these two classes, we start from opposite ends of the lists. I do not propose to discuss the points on which we differ. The evidence on both sides has been published, and also our respective interpretations. Those interested in the question are in a position to form their own judgment on it. The issue will be determined by the results of future research. But Mr. LYON's lucid statement of the case has shown me that my own is obscure in two points, and I wish to take the first opportunity of restating them.

First I wish definitely to disown the suggestion that the fusion of two ancestral cotyledons might have taken place within the seed where they were acting as sucking organs. This appeared in my first sketch of the whole hypothesis, published in May, 1902.<sup>2</sup> In later papers<sup>3</sup> the fusion of the cotyledons is attributed to the reduction of assimilating organs characteristic of geophilous seedlings in their first season, a second suggestion, inconsistent—as Mr. LYON has pointed out—with the first, which is implicitly abandoned. It would have been clearer to state definitely, as I do here, that—if we consider monocotyledons as derived from a dicotyledonous stock by adaptation to a geophilous habit—the fusion of two cotyledons

<sup>1</sup> LYON, HAROLD L., The embryo of the angiosperms. *American Naturalist* 39:13-25. 1905.

<sup>2</sup> The origin of the seed-leaf in monocotyledons. *New Phytologist* 1:107-113. *pls.* 2. 1902.

<sup>3</sup> A theory of the origin of monocotyledons. *Ann. Botany* 17:1-92. *pls.* 1-7. 1903. The evolution of monocotyledons. *BOT. GAZETTE* 37:325-345. 1904.

into one is simply and sufficiently explained by the necessity of reduction in the green parts of the seedling, and that this explanation of course requires that the ancestral cotyledons should be acting as green assimilating organs above ground during the period of fusion, and excludes my first suggestion that they fused as sucking organs within the seed.

That my argument was obscure in a more important respect I infer from Mr. LYON's statement that the evidence on which it is based could as well be read backwards as forwards; in short that the facts on which I rely might be used to prove the derivation of dicotyledons from monocotyledons. My statement of the argument must have been very defective if it admitted of any doubt on this head. No observer dealing with that evidence at first hand could hold such an opinion. He would find the evidence incomplete; he might rate its value much lower than I do; but so far as it goes he must allow that it points in one direction—the derivation of the single from the double cotyledon. To make this clear, the nature of the evidence must be taken into account. It is of three kinds: anatomical, embryological, general.

The anatomical argument is due to Professors QUÉVA and JEFFREY.<sup>4</sup> Both have pointed out that the vascular structure of the young stem in monocotyledons is of the exogenous or dictyoledonous type. They both conclude that monocotyledons are derived from dicotyledons. No botanist, I believe, has denied the facts, which I could confirm if necessary. Their theoretical value may be discounted, but the most ingenious critic could hardly use them to prove the descent of dicotyledons from monocotyledons.

The embryological evidence rests primarily on my conclusion that a certain type of vascular structure in the cotyledon and hypocotyl of liliaceous seedlings is primitive, and that various other types of seedling structure in the same family are genetically connected with it. Where we find a single line of related structures there is nothing—in the absence of independent evidence—to show which of the extreme forms is the more primitive. But where—as in this case—there are several distinct lines of descent ending in the same vascular type, it is fair to assume that type as the primitive structure. For a common ancestor naturally gives rise to divergent stocks, but it would be an extraordinary series of coincidences which should lead several distinct types of structure to produce remote descendants of a single type.

It is true that uniform conditions of life do lead to great superficial resemblance between organs which are morphologically distinct. But

<sup>4</sup> QUÉVA, C., Contributions à l'anatomie des Monocotyledonées, p. 147. 1899.  
JEFFREY, E. C., in COULTER and CHAMBERLAIN'S Morphology of Angiosperms, p. 316. 1903.

the resemblance in such cases is mainly external; the metamorphosis is revealed by differences in internal anatomy. Now in this study of liliaceous seedlings we are dealing with anatomical details which are often uniform, or very nearly so, among allied genera of the most varied external form. Thus, among the Tulipeae some species of *Lilium* have hypogaeic, other species epigaeic cotyledons; the cotyledon of *Fritillaria* is of the common green rush-like form; that of *Tulipa* resembles *Fritillaria*, but the whole structure of the seedling is transformed by the conversion of the stem bud into a dropper. Yet the same vascular symmetry is found in the cotyledon and hypocotyl of all these divergent forms. On the other hand seedlings belonging to almost every tribe of the family possess the green, rush-like cotyledon, but it masks a great variety of vascular structure. Thus the reappearance of definite vascular symmetry in several lines of descent cannot in this case be put down to the action of external conditions moulding distinct types to one pattern. The one simple and adequate explanation of the facts is that the various lines of descent started from a common ancestor with vascular symmetry of this persistent pattern.

Now the whole argument from this class of evidence depends on the fact that this vascular type is bisymmetrical. Two equivalent and quite distinct bundles traverse the elongated cotyledon; two traces in the hypocotyl unite to form a tetrarch root. A single type which is symmetrical about two planes is connected with several symmetrical about one. There is no difficulty in supposing all these unisymmetrical types to be descended from the one bisymmetrical type; but it is incredible that the descendants of distinct unisymmetrical types should all become bisymmetrical structures of precisely the same kind. The argument may be neglected, but it cannot be read backwards. It cannot be used to demonstrate the formation of two cotyledons from one.

I do not mean to assert that the evidence quoted cannot be reconciled with the hypothesis of a primitive monocotylous angiosperm. The bilateral cotyledon may conceivably represent a terminal member which becomes modified in one fashion or another into the likeness of a lateral one. But this interpretation of the facts explains only how an apparently lateral member may be descended from a terminal one. It is a study in the derivation of various monocotylous types from a primitive monocotylous form; it gives no clue to the descent of a race with two cotyledons from that form.

The same criticism applies to that class of evidence which I have called general. My reasons for considering monocotyledons as a race specialized from a dicotylous ancestor by adaptation to the geophilous habit have

already been given in this journal. They need not be repeated here. On that hypothesis the formation of one cotyledon from two is due to the necessity of reduction in the aerial organs of seedling geophytes. The tendency to such reduction is shown in other ways. Among dicotyledons the few species which have but one cotyledon are geophilous, so—with one exception—are those which have cotyledons united almost to the top. In many geophilous forms the cotyledons never appear above ground at all, and the first leaf is much reduced in size. Adaptation to a geophilous habit also serves to explain many of the other structural features which are correlated in monocotyledons with the presence of a single cotyledon, notably the stem anatomy.

But though the collective weight of evidence in favor of this view appears to me very great, I have never thought it conclusive. There are no facts to make it incredible that the primitive angiosperm was monocotylous, and that modern dicotyledons derive their two cotyledons from division of the original member. That opinion, however, cannot be deduced from the evidence just given. It is conceivable that the geophilous habit has served simply to specialize monocotyledons, operating to reduce the original terminal cotyledon to an apparently lateral one. But that hypothesis does nothing to explain the rise of dicotyledons from a monocotylous race, and it leaves the very marked similarity in vascular structure between the primitive liliaceous type and certain geophilous species of Ranales out of the question. Yet the approach to a true monocotyledonous structure in some of these forms is most striking, and extends to the mature as well as the seedling plant.

In conclusion, I wish again to point out that my purpose in this communication has been to correct an inconsistency in the former statement of my argument, and further to restate a portion of it which has been misapprehended. I have purposely abstained from criticism of Mr. LYON's alternative hypothesis, and from any attempt to answer his criticisms on mine, except the two which were founded on obscurity in my previous writings.—ETHEL SARGANT, *Quarry Hill, Reigate, England.*

# CURRENT LITERATURE.

## BOOK REVIEWS.

### A college botany.

PROFESSOR ATKINSON<sup>1</sup> has revised and elaborated his *Elementary Botany* for college use. An elementary college text that includes all of the great divisions of botany seems to be in demand, at least according to the judgment of publishers. Perhaps the demand is both true and just, but it is a large one to make of a single author, who is supposed to be, from the college standpoint, either a morphologist, a physiologist, or an ecologist. One looks for inequality of grasp under such circumstances, unless the presentation is so elementary that it hardly belongs to a modern college course.

In spite of this disadvantage, Professor ATKINSON has covered the whole general field in a way that indicates an unusually wide familiarity with the various divisions of the subject. The parts dealing with physiology and morphology are largely elaborations of the same parts in the elementary text, introducing the new material suited to more advanced students and bringing certain parts up to date. The part dealing with ecology, however, has been entirely reorganized, and represents the first presentation of ecology in an American textbook from the college standpoint.

In the organization of the text, part one (pp. 135) deals with physiology, part two (pp. 207) with morphology, part three (pp. 115) with the ecology of plant members, part four (pp. 184) with plant associations, and part five (pp. 65) with representative families of Angiosperms. The space given to the different parts represents a balance unusually well-maintained for books of this type. There is always a temptation to overdo the part in which the author is especially interested.

Professor ATKINSON believes in numerous and good illustrations, with as many of them original as possible; and hence the volume is full of fresh and suggestive illustrations, and should be of great service to college classes in elementary botany.—J. M. C.

### Handbook of plant morphology.

The friends of ARTHUR, BARNES, and COULTER'S *Handbook of Plant Dissection*, published in 1886, will be glad to know that this helpful laboratory guide has been rewritten, thus bringing it again in touch with the best methods of elementary instruction. The authors have delegated the revision to other hands, and both for this reason and on account of changes necessitated by recent developments in botany, it is perhaps fitting that the new edition should appear under

<sup>1</sup> ATKINSON, GEORGE FRANCIS, A college text-book of botany. pp. xvi + 737. figs. 592. New York: Henry Holt & Co. 1905. \$2.00.



a different title.<sup>1</sup> The most important change noted is the increased number of types discussed, and the presentation of these in a connected account. In harmony with this plan many unrelated details, especially concerning the vegetative structure of the higher plants, are omitted. Though the number of forms discussed is increased from eleven to twenty-five, the size of the book is reduced, having three-fourths the number of pages in *Plant Dissection*. The types selected illustrate very well the probable steps in the evolution of plants, and the discussions are exceedingly clear and suggestive. It seems to the reviewer, however, that the introduction of a heterogamous confervoid form might have strengthened the presentation of the subject of heterogamy among the algae. So long as teachers have too large classes and too little time for purely inductive study in the laboratory, some form of written direction seems indispensable. *Plant Morphology* meets this demand in a most helpful way. A possible danger may lie in its excellence, in that weak teachers may depend upon it too fully and neglect the personal relation which should accompany laboratory study of this character.

—R. B. WYLIE.

#### NOTES FOR STUDENTS.

Allen<sup>2</sup> has recently published in full the results of his study of nuclear division in the pollen mother-cells of *Lilium canadense*, following the preliminary announcement which appeared last year.<sup>3</sup> This paper is of especial interest in relation to the final paper of FARMER and MOORE on the reduction divisions in animals and plants, since Allen reaches fundamentally different conclusions as to the events of synapsis and the preparations for the heterotypic mitosis. As FARMER and MOORE also studied a species of *Lilium* (*L. candidum*), it seems hardly possible that both accounts can be correct, so that the line separating the two schools is sharply drawn in these accounts of a similar form. One school is led by FARMER and MOORE, and finds support in STRASBURGER's recent paper *Ueber reductionsteilung* (1904), and in the recent work of GREGORY on the leptosporangiate ferns, and of WILLIAMS on Dictyota. With ALLEN are associated in the chief point of dispute (the formation of the bivalent chromosomes of the heterotypic mitosis) the botanists of the Carnoy Institute, GREGOIRE and BERGHS, and also ROSENBERG.

ALLEN's account is chiefly remarkable for the detailed study of the events preceding and following synapsis, which are presented in greater detail than in any previous investigation. The nucleus of the young pollen mother-cell contains a network of large irregular masses, derived from the chromosomes of the preceding mitosis in the archesporium, and connected by fibers. As the nucleus increases in size, the chromatin knots become widely separated, and the nucleoli

<sup>1</sup> CALDWELL, O. W., *Handbook of Plant Morphology*. 12mo. pp. viii + 190. New York: Henry Holt & Co. 1904.

<sup>2</sup> ALLEN, C. E., Nuclear division in the pollen mother-cells of *Lilium canadense*. *Annals of Botany* 19:189-258. pls. 6-9. 1905.

<sup>3</sup> BOTANICAL GAZETTE 37:464. 1894.

are clearly distinct from the network. During synapsis the reticulum becomes transformed into a definite spirem, the fibers thickening apparently by the distribution of material from the knots, which become less conspicuous. The fibers now arrange themselves in pairs, and a general contraction of the reticulum takes place, probably associated with this approximation of the fibers. There is thus formed a continuous spirem in the nucleus, which is plainly composed of two slender threads lying side by side and probably with no free ends. The two threads often run closely parallel, sometimes loosely twisted about one another, sometimes in contact and apparently fused, and sometimes rather widely separated. It is clear that the double nature of the spirem is not due to a fission, but that two independent threads are developed out of the reticulum. The two threads are regarded as of paternal and maternal origin respectively. They gradually fuse, so that in later stages of synapsis the nucleus appears to contain a relatively thick single (fusion) spirem, which is shorter and more loosely coiled than in earlier stages. Each thread of the pair consists of a series of chromatin granules (chromomeres) imbedded in a ground substance (linin). As the two threads unite, the chromomeres generally come together in pairs and fuse to form a single row of larger chromomeres. The single (fusion) spirem on emerging from synapsis becomes uniformly distributed throughout the nucleus as a much convoluted thread. Some of the loops become fastened to the periphery of the nucleus. There is no regularity in the number of chromatic segments which are formed later.

While evenly distributed the single (fusion) spirem undergoes a longitudinal fusion into two threads, which is preceded by a division of each fusion chromomere. This is the first longitudinal fusion, well known from the descriptions of GREGOIRE, GUIGNARD, MORTIER, and others. The split spirem now segments into the reduced number of chromatic elements (bivalent chromosomes) characteristic of the heterotypic mitosis. The first free ends of the segments usually appear at the periphery of the nucleus, where it is evident that the split spirem breaks apart at the loops. The segments of the split spirem now shorten and thicken, taking on the various forms peculiar to the heterotypic mitosis. They are obviously pairs of chromosomes, which stand for the full number of sporophytic elements (24), now associated to form a reduced number (12) of bivalent chromosomes. Shortly after the segmentation of the spirem the chromosomes of each pair may show evidence of the second longitudinal fission, which is completed during the metaphase of the heterotypic mitosis. Meanwhile the spindle of the heterotypic mitosis is being organized, the position of the bivalent chromosomes is shifted, and they are arranged on the nuclear plate where the elements of each pair separate as the so-called daughter chromosomes of the heterotypic mitosis. This first division in the spore mother-cell then simply distributes in two sets the twenty-four sporophytic chromosomes which ALLEN believes to have been derived from a maternal and paternal spirem. The second longitudinal fission which becomes conspicuous during metaphase of the heterotypic mitosis is clearly a premature fission of the chromosomes which are to enter the second nuclear

division (homotypic). There is no true resting period between the two mitoses, and the chromosomes which leave the heterotypic figure pass morphologically unchanged into the homotypic.

The chief points of difference between ALLEN's account and that of FARMER and MOORE are briefly as follows: FARMER and MOORE fail to find the organization of two threads preliminary to the formation of the single spirem which emerges from synapsis. They recognize only one longitudinal fusion of this spirem, which is regarded as preliminary to the formation of the chromosomes of the homotypic mitosis. The pairs of chromosomes of the heterotypic mitosis are believed to arise by the approximation of the arms of loops and their separation at the head. The theoretical aspects of these two views in relation to the significance of the reducing division cannot be considered here. The accounts themselves rest on matters of fact and not of interpretation, and one or the other is likely to fall, for it is hardly possible that both can be right, especially since they treat of the same form.

ALLEN presents at the end of his paper a thorough and very interesting discussion of his conclusions in their relation to problems of heredity and hybridization.—B. M. DAVIS.

THE SUBJECT of soil inoculation for legumes has recently acquired a widespread interest in this country, first, from numerous popular accounts relating to the subject, and again on account of a widely advertised commercial product by which is it claimed the proper bacteria can be introduced into the soil. For this reason MOORE's account<sup>4</sup> of his work in this field is of special interest. The first part of the bulletin is a general historical account dealing with the various methods by which nitrogen is fixed in the soil, and leading up to the discoveries of HELRIGEL and WILLFARTH connecting the fixation of nitrogen by legumes with the tubercles on the roots, and the discovery of bacteria in these tubercles by WORONIN. The chief results of MOORE's investigations may be briefly stated as follows. The root-tubercle organism exists in three well-defined forms. In the soil it has the form of extremely minute motile rods. These possess the power of infecting the root hairs of leguminous plants. Within the root the organisms multiply enormously and produce the hypha-like "infection threads" passing through the tissues of the host. These curious fungus-like structures have often been observed and figured, and have been the objects of much discussion. Their explanation is that they are zooglaea-masses composed of numerous minute bacteria. These minute bacteria soon give rise to larger rod-shaped forms which may or may not be motile. These finally produce the branched forms peculiar to the legume-nodule. It is only this last form that is of any benefit to the plants, for in this state the bacteria are broken down and their contents made available. The name of the organism is changed to *Pseudomonas radiculicola*, since the motile rods have flagellae only on one end. There

<sup>4</sup> MOORE, G. T., Soil inoculation for legumes, etc., U. S. Dept. of Agric., Bureau of Plant Industry, Bull. 71, pp. 72. pls. 10. 1905.

is only a single species, but several forms or races occur adapted to certain species of legumes. Their slight racial characteristics may be easily broken down by cultivation. The results of studies on the nitrogen-fixing power of the bacteria are extremely interesting, showing that the supposed symbiotic relation between the organism and the root probably does not exist. It is rather to be regarded as a parasite, its nitrogen value being merely incidental to the death of the organism. The nitrogen is fixed by the tubercle-forming bacteria within their bodies. This was determined by cultures in flasks containing nutrient solutions without nitrogen. There was no increase of nitrogen in the solution, but a marked increase in the organisms themselves. In its biology the organism is therefore considered a parasite. Later the plant is able to overcome the parasite and profit by the nitrogen which has been fixed. When grown on nitrogenous media, it was found that the organism lost both its power of infecting leguminous plants and its power of fixing nitrogen. In non-nitrogenous media both of these properties were retained. The failure of NOBBE's attempts in Germany a few years ago to put upon the market pure cultures of this organism can probably be attributed to lack of recognition of this fact. As a result of these studies MOORE has devised a method of putting up for distribution pure cultures of *Pseudomonas radiclepla*, grown in nitrogen-free media and dried on cotton immersed in the culture. These cultures are sent out by the U. S. Department of Agriculture together with packages of nutrient salts to multiply the organism. The mass-culture thus obtained is used to inoculate the seed or the soil. Numerous reports from farmers of all states indicate that this method will prove successful and practicable.<sup>5</sup>—H. HASSELBRING.

WÄCHTER<sup>6</sup> has endeavored to solve some of the problems arising from the investigations of PURIEWITSCH on the autodepletion of storage organs. The latter author found inorganic salt solutions to behave as isotonic sugar solutions in accomplishing an inhibition of autodepletion. For this fact PURIEWITSCH accounted by assuming an incipient plasmolysis of the protoplasm, and in cases where inhibition is accomplished by dilute salt solutions he resorted to a fluctuating permeability of the plasma for explanation. WÄCHTER is apparently skeptical of both explanations. For his material the author selected the onion, expecting to avoid such difficulties as are associated with the inversion of insoluble storage products, being able thus to deal only with diosmosing substance, which was supposed to be chiefly glucose in the onion. He finds, however, that glucose is not the chief storage product; that other not directly reducing carbohydrates are present in fully equal amount, and that they exosmose into water or into salt solution in far greater proportion than does the glucose. For this fact the author

<sup>5</sup> By an oversight, only a portion of this review appeared in the BOTANICAL GAZETTE for May, p. 371.—EDS.

<sup>6</sup> WÄCHTER, W., Untersuchungen über den Austritt von Zucker aus den Zellen der Speicherorgane von *Allium Cepa* und *Beta vulgaris*. Jahrb. Wiss. Bot. 41:165-220. fig. 1. 1905.

remains unable to account. Attempts to correlate with external conditions the relative amounts of reducing and non-reducing sugar exosmosing were unsuccessful. Further experiments indicate that only a partial depletion of such storage organs is possible, while PURIÉWITSCH believed complete depletion possible. WÄCHTER believes from his results that the density of the external medium is not a factor in depletion, for he found that even with exosmosis inhibited the density of the cell sap was greater than that of the external fluid. The author remains uncommitted as to the fluctuating permeability of the plasma, and insists that further investigation is necessary to answer this question.—RAYMOND H. POND.

THE X-GENERATION and the 2x-generation is the title of an interesting philosophical paper by LOTSY.<sup>7</sup> The nuclei of the x-generation contains only one-half the number of chromosomes as do the nuclei of the 2x-generation. Only asexually reproducing organisms have the x-number of chromosomes. Then which generation should be called the x-generation? If the fern plant is the x-generation, the prothallium is a  $\frac{1}{2}$ x-generation; if the prothallium is the x-generation, the fern plant is a 2x-generation. The behavior of the chromatin during fertilization and during the reduction of chromosomes shows that the x-generation is the primitive generation, and that the 2x-generation is later, and that its double number of chromosomes is due to fertilization. Thus the ancient question of the philosophers, which came first, the hen or the egg, can be answered by merely counting the chromosomes. The 2x-generation cannot exist indefinitely, but sooner or later must form reproductive cells in which the primitive number of chromosomes is restored. This reversion to the x-generation consists in the separation of the paternal and maternal chromosomes. The process is preceded by the pairing of these chromosomes, which have remained separated throughout the vegetative life of the organism. Numerical reduction of chromosomes is the expression of this pairing. LOTSY does not hesitate to apply the theory to animals, the body representing the 2x-generation, while the x-generation is reduced to the sexual cells.—C. J. CHAMBERLAIN.

THOMSON<sup>8</sup> has been investigating the megaspore membrane or coat of gymnosperms, naturally applying the term to the investing coat of the prothallium as well as to the coat of the uninucleate spore. This coat is present in all gymnosperms except the Taxeae, among which it is entirely eliminated or nearly so. It consists of two layers, the outer one being suberized, while the inner one is composite in character, being suberized in its outer portion and containing cellulose in its inner portion associated with a substance resembling pectin. In fact, the megaspore coat resembles in structure and composition the microspore coat. The only exception to this general character of the megaspore coat is found among

<sup>7</sup> LOTSY, J. P., Die x-Generation und die 2x-Generation, eine Arbeitshypothese. Biol. Centralbl. 25:97-117. 4 diagrams. 1905.

<sup>8</sup> THOMSON, R. B., The megaspore-membrane of the gymnosperms. Univ. of Toronto Biol. Series, No. 4, pp. 64. pls. 5. 1905.

the Araucariae, where the suberized outer layer is wanting. In the forms possessing the usual type of membrane, there is present a more or less well-developed tapetum, derived from the sporogenous tissue, which is quite distinct from that derived from nucellar tissue. Using the relative development of the megaspore coat and of the tapetum as a basis, the author concludes that the Abietae are the most ancient group of Coniferales and the Taxeae the most recent; that the Taxodiaceae and Podocarpeae are complex, including both ancient and recent forms; and that the Cupresseae occupy an intermediate position in the phylogenetic series.—J. M. C.

NICOLOSI RONCATI<sup>9</sup> has published an account of the ovule of *Anona Cherimolia*. A row of four megaspores and considerable parietal tissue are formed. The innermost megaspore develops a narrow and much elongated embryo sac, whose antipodals appear to be ephemeral. The first divisions of the endosperm cells result in a series of walls across the narrow sac, which is thus divided into a linear series of five or six large chambers. Subsequent divisions fill these chambers with endosperm tissue. The embryo, as figured, has no definite suspensor, but is at first a globular mass of cells. The "rumination of the seed," characteristic of Anonaceae, is attributed by the author to the invasion of the perisperm by infoldings, chiefly from the inner integument. If this be true, it is entirely different from the "rumination" to be observed in *Asimina* and in *Torreya*. The name "reserve idioblasts" is given to masses of nutritive material found in abundance in cells along the convolutions of the "rumination," and thought to supply nutrition to the embryo after the endosperm has been digested and the perisperm contains an insufficient nutritive supply. The paper was presented to the Academy by Professor CAVARA.—J. M. C.

JONES<sup>10</sup> has published an account of the anatomy of the stem of *Lycopodium*. The general conclusions reached are as follows: The development of the vascular system has proceeded along two lines: (1) as the protoxylems increase in number, a series of alternating bands of xylem and phloem is developed; (2) the phloem is scattered through the mass of xylem in more or less isolated patches, until a structure is produced that simulates that of *Gleichenia*. The first form is developed in creeping stems, the second is characteristic of tropical epiphytes. The young stem has a triarch or tetrarch structure; and the complex structure of larger stems is developed from this by the division of one of the protoxylems into two strands, and by the separation of a phloem into two portions; subsequently, another protoxylem divides, and this process, together with the splitting of the phloem, is repeated until the number of protoxylems and protophloems reaches the number present in the large stem. The disposition of xylem and phloem is constantly altering, the length through which a definite portion of tissue (as a phloem-island) may be traced varying from 0.5 to 8mm.—J. M. C.

<sup>9</sup> RONCATI, F. NICOLosi, Sviluppo dell' ovulo e del seme nella *Anona Cherimolia* Mill. Atti Acad. Gioenia Sci. Nat. Catania IV. 18: Mem. 2. pp. 26. pl. 1. 1904.

<sup>10</sup> JONES, CHARLES EDWARD, The morphology and anatomy of the stem of the genus *Lycopodium*. Trans. Linn. Soc. London. II. Bot. 7: 15-35. pls. 3-5. 1905.

ROSE has published a fourth paper under the title "Studies of Mexican and Central American plants."<sup>11</sup> The contribution involves twenty-three families, under which the miscellaneous titles are grouped. Two new genera are described, one (*Ornithocarpa*) in Cruciferae, the other (*Raimannia*) in Onagraceae. The new species described belong to *Ostrya* (2), *Synthlipsis*, *Thelypodium*, *Lepidium*, *Echeveria* (2), *Ribes* (7), *Neptunia*, *Cercidium* (3), *Parosela* (12), *Lupinus* (16), *Indigofera* (4), *Phaseolus* (3), *Aeschynomene*, *Cologania*, *Crotalaria*, *Harpalyce*, *Willardia*, *Erythroxylon* (3), *Cedrela*, *Polygala*, *Vitis*, *Heliocarpus* (3), *Tilia* (2), *Abutilon* (3), *Kosteletzkya* (2), *Robinsonella* (2), *Ceiba* (2), *Ayenia* (2), *Melochia*, *Taonabo* (3), *Heterocentron*, *Conostegia*, *Monochaetum*, *Hartmannia* (3), *Raimannia* (3), *Eryngium* (6), *Prionosciadium* (5), *Arracacia*, *Coulterophytum*, *Ligusticum*, *Musenopsis* (2), *Oaxacana*, *Roseanthus*, and *Schizocarpum*. The new genus *Raimannia* replaces *Oenothera* as recently understood, twelve species being given as belonging to it; and the name *Oenothera* replaces *Onagra*. There is also a synopsis of the Mexican species of *Ribes*.—J. M. C.

OAKES AMES<sup>12</sup> has begun a sumptuous series of publications dealing with the taxonomy of Orchidaceae. Its purpose is "to illustrate, from type material when possible, new or recently described orchid species, and species heretofore inadequately figured; to publish the original descriptions of all species so figured, with additional characterization, full synonymy, and geographical distribution; to furnish descriptions and descriptive lists of orchidaceous plants, which may prove useful in the study of regional floras; and to communicate the results of critical investigations among special genera." In the first fascicle nineteen species are described and illustrated, five of which are new, the plates being drawn by Blanche Ames and made by the Heliotype Company. There are also the following contents: A descriptive list of orchidaceous plants collected in the Philippine Islands by botanists of the U. S. Government (including sixteen new species); an *Oncidium* new to the United States; Contributions toward a monograph of the American species of *Spiranthes*; and A synopsis of the genus *Spiranthes* north of Mexico.—J. M. C.

KIENTZ-GERLOFF<sup>13</sup> has published a small book dealing with bacteriology. As indicated by the title, it gives a general condensed view of the modern field of bacteriology in its relation to the home, the kitchen, the dairy, etc. A general introduction deals with the evolution of the modern theory of fermentation

<sup>11</sup> ROSE, J. N., Studies of Mexican and Central American plants. Contrib. U. S. Nat. Herb. 8:281-339. pls. 63-72. figs. 14-19. 1905.

<sup>12</sup> AMES, OAKES, Orchidaceae: illustrations and studies of the family Orchidaceae issuing from the Ames Botanical Laboratory, North Easton, Mass. Fasc. I. pp. vii+156. pls. 16. Boston and New York: Houghton, Mifflin and Company. 1905.

<sup>13</sup> KIENTZ-GERLOFF, FELIX, Bakterien und Hefen insbesondere in ihren Beziehungen zur Haus- und Landwirtschaft zu den Gewerben, sowie zur Gesundheitspflege nach dem gegenwärtigen Stande der Wissenschaft gemeinverständlich dargestellt. 8vo. pp. 100. Berlin: Otto Salle. 1904.

as resulting from PASTEUR'S work on spontaneous generation. An insight is given into the relations of molds, fungi, bacteria, and yeasts to each other, with an outline of their general morphology and classification. Modern methods of cultivation and the introduction of pure cultures in fermentation industries and dairies are discussed. A short chapter is devoted to the activity of bacteria in the soil and their relation to agriculture. Considerable space is finally devoted to pathogens, and the spread of infectious and contagious diseases. Advice and methods are given as to their prevention and treatment. A number of illustrations elucidate the text. The whole book represents a good summary of our present knowledge of micro-organisms in a concise, popular style.—P. HEINEMANN.

GOEBEL<sup>14</sup> has investigated the cleistogamous flowers of a variety of plants from the point of view especially of the adaptation theory, and presents an interesting account of the external condition under which these occur in nature, or can be made to occur in culture. It appears that a large number of plants have the ability to produce cleistogamous instead of chasmogamous flowers under the influence of certain external conditions. Contrary to the belief of DARWIN and others, GOEBEL shows that there is no causal connection between the absence of fertilization, or the formation of seed, and the appearance of cleistogamous flowers. The latter is due to insufficient food relations, and this may arise from poor soil, a lack of mineral constituents, or insufficient light. In many plants the cleistogamous flowers do not set seed. In these cases the appearance of cleistogamous flowers is not due to the suppression of seed-formation, but GOEBEL thinks the seed-formation is suppressed by the appearance of cleistogamous flowers.—W. B. MCCALLUM.

MOLISCH<sup>15</sup> has reported convincing evidence that stems of certain seedlings respond with positive curvatures when exposed to rays emanating from sealed tubes containing a mixture of radium and zincsulfid. The seedlings should be less than 7<sup>cm</sup> distant from the tubes and preferably about 2<sup>cm</sup>. Tubes containing radium bromid only (activity 3000) fail to give positive results, as previously found by DIXON. When radium bromid and zincsulfid are mixed, however, a steady phosphorescence of considerable intensity develops, due to the influence of the radium on the zincsulfid. MOLISCH therefore regards the curves obtained as heliotropic, indirectly induced by radium. The interesting fact is also recorded that while such experiments succeed in the laboratory they usually fail in the greenhouse. The author believes that the illuminating gas and other volatile impurities in laboratory air reduce the negative geotropism, thereby increasing sensitiveness to phosphorescence and heliotropic stimulus.—RAYMOND H. POND.

<sup>14</sup> GOEBEL, K., Die kleistogamen Blüten und die Anpassungstheorie. Biol. Centralbl. 24:673-697, etc. 1904.

<sup>15</sup> MOLISCH, HANS, Ueber Heliotropismus, indirekt hervorgerufen durch Radium. Ber. Deutsch. Bot. Gesells. 23:2-7. fig. 1. 1905.



THE FIRST CASE of the regeneration of the whole plant from tendrils is described by WINKLER.<sup>16</sup> VÖCHTING first showed that the tendrils of *Vitis vinifera* will produce roots, but on *Passiflora coerulea* WINKLER finds that the isolated tendrils will give rise to both roots and shoots. Young tendrils were cut off and placed in damp sand. They continued to live, but soon became quite woody, and in the course of some weeks formed a callus at the base. After three or four months a root is formed from this callus, and after some months more two shoots arise, also from the callus. The leaves of this plant also form roots and shoots in the same way when similarly treated. The fact is pointed out that the shoots formed from the primary undivided leaves continue to form primary leaves much longer than those formed on the adult leaves. On isolated pieces of stem internodes new shoots arise from the callus at the base.—W. B. McCALLUM.

POURIEVITCH<sup>17</sup> shows by experiment that the investigations of BONNIER, and MANGIN which have been the basis for the prevailing opinion that the ratio  $\frac{\text{CO}_2}{\text{O}_2}$  does not vary with temperature include some errors, namely comparisons of incomparable material, and tests of too short duration to permit the test objects to acquire the temperature intended for the test. From his own investigations, in which such errors and others are apparently avoided, the author concludes that the ratio  $\frac{\text{CO}_2}{\text{O}_2}$  changes according to temperature, becoming greater as the latter rises. This influence of temperature is most noticeable in young organs, and depends upon the kind of nutritive substance present in the tissues. When this nutritive substance disappears from the tissue, the influence of temperature on the ratio  $\frac{\text{CO}_2}{\text{O}_2}$  becomes less noticeable.—RAYMOND H. POND.

SPALDING showed that when roots are wounded near the tip and traumatropic curvature prevented by placing them in plaster for as long as eight days, they will when removed from the plaster curve in the same way and with the same reaction time as they would have done had they been allowed to do so at first. He considers that the latent period has been prolonged all this time. BURNS<sup>18</sup> has reinvestigated this problem and finds that so long as the wounded tissue persists the stimulus to traumatropic curvature still exists, and unless mechanically prevented the root will curve. When regeneration of the wounded tissue is completed the stimulus is removed. There is thus not a prolongation of the latent period, but a continuation of the stimulus.—W. B. McCALLUM.

<sup>16</sup> WINKLER, H., Ueber regenerative Sprossbildung an der Ranken, Blättern und Internodien von *Passiflora coerulea* L. Ber. Deutsch. Bot. Gesells. 23:45-48. 1905.

<sup>17</sup> POURIEVITCH, M. K., Influence de la température sur la respiration des plantes. Ann. Sci. Nat. Bot. IX. 1:1-32. 1905.

<sup>18</sup> BURNS, G. P., Regeneration and its relation to traumatropism. Beih. Bot. Centralbl. 28:159-164. figs. 4. 1904.

PRIANISCHNIKOW<sup>19</sup> presents a preliminary report of sand culture experiments which extend his investigations of 1900 on the relative value of different phosphates in plant nutrition. As in the earlier work he found ammonium sulfate to be a "physiologically acid" salt, so now he finds, contrary to all expectations, that ammonium nitrate can also function as a "physiologically acid" salt. This peculiar acidity is much less in the case of ammonium nitrate, however, than in that of ammonium sulfate. The phrase "physiologically acid" is used in the sense suggested by ADOLPH MEYER as applied to a salt whose basic group is more rapidly appropriated by the plant than its acid group.—RAYMOND H. POND.

WORSDELL<sup>20</sup> has discussed the meaning and origin of the phenomenon ordinarily called fasciation, including not merely those abnormal appearances to which the term is ordinarily applied, but also "normal fasciation" as exemplified by such stamen clusters as appear in Hypericaceae and Malvaceae. His contention is that in the development of a structure there are two opposing tendencies, the younger being a tendency to integrity, the latter being a tendency to plurality, and that the condition of the mature structure is the resultant. The mechanical cause suggested has to do with the distribution and functioning of "growth centers."—J. M. C.

PINCHOT<sup>21</sup> has published a second part of his *Primer of Forestry*, dealing with the practice of forestry, work in the woods, and the relation of the forest to weather and streams. There is also a short account of forestry at home and abroad. Numerous reproductions from photographs fill out what is a very satisfactory elementary account of practical forestry. Such literature, prepared by those who have the most ample information, will do more than anything else to educate the intelligent public as to the meaning and need of forestry.—J. M. C.

A GENERAL ACCOUNT of the vegetation of the island of Guam has been published by W. E. SAFFORD.<sup>22</sup> The account includes some reference to every plant known to occur on the island, and discusses the principal plants used for food, fiber, oil, starch, sugar, and forage in the Pacific tropical islands recently acquired by the United States. The method of cultivating and propagating the more important species is treated in considerable detail. While the paper is somewhat miscellaneous as to contents, it is full of information for botanists.—J. M. C.

<sup>19</sup> PRIANISCHNIKOW, D., Ueber den Einfluss von Ammoniumsalzen auf die Aufnahme von Phosphorsäure bei höheren Pflanzen. Ber. Deutsch. Bot. Gesells. 23:8-17. 1905.

<sup>20</sup> WORSDELL, W. C., "Fasciation:" its meaning and origin. New Phytologist 4:55-74. figs. 17-24. 1905.

<sup>21</sup> PINCHOT, GIFFORD, A primer of forestry. Part II. Practical forestry. U. S. Department of Agriculture, Bureau of Forestry, Bull. 24. part 2. pp. 88. 1905.

<sup>22</sup> SAFFORD, WILLIAM EDWIN, The useful plants of the island of Guam, with an introductory account of the physical features and natural history of the island, of the character and history of its people, and of their agriculture. Contrib. U. S. Nat. Herb. 9:1-416. pls. 1-69. 1905.

A SMALL MANUAL of poisonous plants has been prepared by A. BERNHARD SMITH.<sup>23</sup> It contains plants from all countries, with their active principles and toxic symptoms, together with the proper treatment in case of poisoning. The main divisions are four in number: (1) plants acting on the brain; (2) those acting on the spinal cord; (3) those acting on the heart; and (4) vegetable irritants. Subdivisions on the basis of symptoms lead one easily to the different groups of plants.—J. M. C.

THE RECENT ADDRESS of Professor D. H. SCOTT as president of the Royal Microscopical Society dealt with the subject of the so-called Carboniferous ferns,<sup>24</sup> which comprise about half of the total known flora. The recent discoveries of seed-bearing forms among them were reviewed, and the conclusion reached that in all probability only a minority of these reputed ferns are really ferns, and that probably the majority of them are seed-bearing plants.—J. M. C.

ARBER<sup>25</sup> has described two new species of the seed-genus *Lagenostoma*, whose chief interest is its relation to *Lyginodendron*. An important point in connection with these new species is that the seeds, "with or without a cupular investment," terminate the ultimate branches of what is probably a modified fertile leaf.—J. M. C.

JOHNSTON<sup>26</sup> has published thirty-five new species preliminary to the publication of a flora of the Islands of Margarita and Coche, Venezuela. Among them there is a new genus (*Anguriopsis*) of Cucurbitaceae.—J. M. C.

IN CONTINUING his revision of *Eucalyptus*, MAIDEN<sup>27</sup> presents *E. amygdalina*, *E. linearis*, and *E. Risdoni*, under each species giving the description, synonymy, range, and affinity.—J. M. C.

SMITH<sup>28</sup> has published an account of three diseases of truck crops in Delaware: (1) a leaf-spot of cucumber, squash, melon, and cantaloupe due to *Sphaerella citrullina*; (2) a leaf-spot of the egg-plant due to *Ascochyta lycopersici*; and (3)

<sup>23</sup> SMITH, A. BERNHARD, Poisonous plants of all countries. pp. xv+88. Bristol: John Wright & Co. 1905.

<sup>24</sup> SCOTT, DUKINFELD H., What were the Carboniferous ferns? Jour. Roy. Micr. Soc. 1905: 137-149. pls. 1-3. figs. 32-33.

<sup>25</sup> ARBER, E. A. NEWELL, On some new species of *Lagenostoma*: a type of pteridospermous seed from the Coal-measures (abstract). Annals of Botany 19:326-328. 1905.

<sup>26</sup> JOHNSTON, J. R., New plants from the islands of Margarita and Coche, Venezuela. Proc. Amer. Acad. 40:683-698. 1905.

<sup>27</sup> MAIDEN, J. H., A critical revision of the genus *Eucalyptus*. Part VI. pls. 4. Published by the authority of the Government of the State of New South Wales. 1905. 2s. 6d.

<sup>28</sup> SMITH, C. O., The study of the diseases of some truck crops in Delaware. Bull. Del. Exp. Sta. 70. pp. 16. pls. 2. figs. 6. 1905.

a leaf-spot of the bean and cow pea due to *Phyllosticta phaseolina*. Brief descriptions are given in each case of the fungus itself and its behavior in pure cultures and inoculation experiments. No experiments in the treatment of these diseases are reported. The paper should be of interest to mycologists.—E. MEAD WILCOX.

ROLFS<sup>29</sup> has published his second contribution to the knowledge of a potato disease, called the rosette by SELBY,<sup>30</sup> due to the sterile fungus *Rhizoctonia*. The author has conducted extensive experiments both in the treatment of the disease and in the study of the life history of the fungus. He finds that the corticium or fruiting stage of the fungus develops freely upon the living stems of the diseased plants, but considers the sclerotial bodies which are common on both stems and tubers the most important agents in the distribution of the fungus. Formalin treatment of the tubers to be planted improved the appearance of the crop but reduced the yield. The corrosive sublimate solution treatment gave good returns when the land employed for the crop was new. Liming the soil and treating the "seed" tubers with sulfur gave negative results. The following recommendations are also made: (1) clean tubers should be carefully selected from healthy tubers for planting, (2) all vines and stems of weeds should be gathered and burned at the end of the season, (3) care must be taken to see that the fertility of the soil is maintained, that through proper methods of cultivation the soil is well aerated, and that where irrigation is employed the water is applied to the land at frequent intervals and in proper amounts, taking care not to allow the soil immediately about the forming tubers to become too wet.—E. MEAD WILCOX.

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<sup>29</sup> ROLFS, F. M., Potato failures. A second report. Bull. Col. Exp. Sta. 91. pp. 33. pls. 5. 1904. See Bull. 70 Col. Exp. Sta. for the preliminary report upon this subject.

<sup>30</sup> See Bulletins 139 and 145 of the Ohio Experiment Station.

## NEWS.

F. C. NEWCOMBE has been advanced to a full professorship of botany at the University of Michigan.

F. E. CLEMENTS, University of Nebraska, has been appointed associate professor of plant physiology.

PROFESSOR F. W. OLIVER, University College, London, has been elected a Fellow of the Royal Society.

JULIUS WIESNER, University of Vienna, has been elected member of the Royal Danish Academy of Science.

N. WILLE, University of Christiania, has been elected foreign member of the Academy of Sciences at Stockholm.

DR. F. DELPINO, professor of Botany in the University and Director of the Botanic Garden, died at Naples May 14.

IDA E. CAROTHERS, University of Chicago, has been appointed instructor in botany at Rockford College, Rockford, Ill.

F. GRACE SMITH, University of Chicago, has been appointed instructor in botany at Smith College, Northampton, Mass.

P. H. OLSSON-SEFFER, Stanford University, is to spend three months in the province of Soconusco, Mexico, in experimental work upon the Mexican rubber tree.

F. D. HEALD, University of Nebraska, has been appointed botanist of the Agricultural Experiment Station and Associate Professor of botany in the University School of Agriculture.

DR. W. B. MCCALLUM, University of Chicago, has received the first Walker prize from the Boston Society of Natural History, the title of his paper being "Physiological analysis of the phenomena of regeneration in plants."

THE BIOLOGICAL STATION of the University of Montana, under the directorship of M. J. Elrod, has announced its seventh annual session at Flathead Lake, Bigfork, Montana, extending from July 12 to August 17. The work in botany will be under the direction of Thomas A. Bonser (University of Chicago) of Spokane.

THE MINNESOTA SEASIDE STATION, under the directorship of Professor Conway MacMillan, has announced its fifth session at Port Renfrew, British Columbia, on the Straits of Juan de Fuca. The session extends from July 8 to August 18, and the botanical staff consists of Conway MacMillan, Albert Schneider, Josephine E. Tilden, and F. K. Butters.

## GENERAL INDEX.

The most important classified entries will be found under Contributors, Personals, and Reviews. New names and names of new genera, species, and varieties are printed in **bold-face** type; synonyms in *italics*.

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